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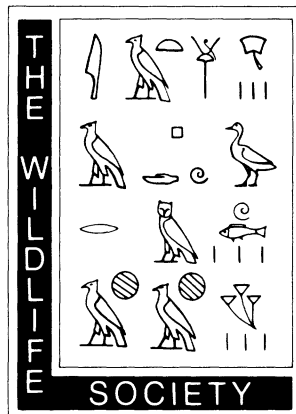
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## **USE OF SNAGS BY CAVITY-NESTING BIRDS IN THE SIERRA NEVADA**

by

MARTIN G. RAPHAEL AND MARSHALL WHITE

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FRONTISPIECE. The northern flicker (*Colaptes auratus*), an abundant cavity-nesting bird in burned forests of the Sierra Nevada, excavates nest holes in well-decayed, older snags. (Photo by M. G. Raphael)

# USE OF SNAGS BY CAVITY-NESTING BIRDS IN THE SIERRA NEVADA

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**Abstract:** We studied nesting and foraging habitat selection by cavity-nesting birds (CNB) in burned and unburned Sierra Nevada forests during spring and summer from 1975 through 1979. We located 561 active nests of 18 CNB species, including 9 excavators. Characteristics of nest trees were compared among bird species and to a sample of available trees using univariate and multivariate analyses. Overall, 72% of the nests were in standing dead trees (snags), whereas only 7% of available standing trees were dead. Compared to available trees, nest trees were larger in diameter, surrounded by a larger number of snags >23 cm diameter at breast height (dbh), had more bark cover, and were more often broken-topped white fir (*Abies concolor*). Diameter was the most consistently important difference observed between nest trees and trees available to each bird species. Comparisons of nest sites among bird species showed that tree height varied most. Interspecific differences in nest hole height were completely explained by these tree height differences. Bird species also differed in their preferences for tree decay-states. Bark-gleaning species tended to nest in well-decayed, softer snags; timber-drilling species nested in sounder snags. These differences suggested that little interspecific competition for nest sites occurred in this bird community. Two sapsucker species may have competed because their nesting habitat and preferred trees were similar; all other species used different kinds of trees or nested in different habitat types. Most (67%) of the nest cavities occupied by nonexcavators were created by excavators (woodpeckers and nuthatches). Brown creepers (*Certhia americana*) did not depend on excavators for holes and chose trees that were different from those of other CNB.

We recorded 1,026 foraging behavior observations of 10 bird species. All species except brown creepers and pygmy nuthatches (*Sitta pygmaea*) and red-breasted nuthatches (*S. canadensis*) foraged on snags more often than predicted from snag availability. Birds preferred to forage on trees 23–53 cm dbh; morphologically similar species tended to feed at different tree heights. However, differences in foraging method, rather than differences in microhabitat, were more responsible for foraging segregation.

Cavity-nesting bird density increased in proportion to snag density on 7 study plots. CNB density declined 77% after snag removal on a burned plot, but 2 CNB species nested in remaining stumps. Density of CNB varied from 19 to 65 pairs/40 ha on 6 other plots and was most strongly correlated with density of snags >38 cm dbh. CNB density was not correlated with any live vegetation variable. Yearly changes in CNB density from 1966 through 1979 were highly negatively correlated with annual precipitation. Winter weather apparently influenced density through direct mortality or by inducing movements to or from the study plots, suggesting that winter habitat may be critical.

We estimated that 423 suitable soft snags (15 years or older) per 40 ha were required to support maximum bird densities on burned forests and that 4 hard snags were required to produce 1 soft snag. On unburned forests, 342 suitable snags (one-third hard) were required/40 ha. Snag suitability could be predicted using diameter, bark cover, and top condition. Snags should be managed as dispersed clumps rather than as isolated individuals to meet nesting and feeding requirements. Providing sufficient numbers of large-diameter snags on managed stands often will require retention of trees and selected stands beyond the usual rotation period or retention of existing patches of old-growth timber. Recommendations for future research emphasize winter habitat studies and more detailed nesting and foraging studies.

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## INTRODUCTION

Snags occur when standing trees die, principally from injury, suppression, fire, lightning, disease, insect infestation, and weather extremes (Mannan et al. 1980). In managed forests, especially in the western United States, snags and dying trees often are felled to prevent fire or safety risks, to control injurious insects, or to eliminate conflicts with other management activities. Increasingly, snags are harvested for lumber (Fahey 1977, Snellgrove 1977, Snellgrove and Fahey 1977, Sickie and Benson 1978), pulp (Lowery et al. 1977), and fuel (U.S. Forest Service 1976). There are fewer snags in managed forests than in unmanaged forests (Cline et al. 1980).

Many recent studies document wide-

spread use of snags by wildlife, especially birds (Conner 1973; Gale 1973; Beebe 1974; Jackman 1974; Balda 1975a,b; Conner et al. 1975; McClelland and Frissell 1975; Boyer 1976; Study Committee on Snags 1976; Thomas et al. 1976; Cline 1977; Hardin and Evans 1977; McClelland 1977; Scott et al. 1977; Bull 1978; Conner 1978; Raphael and White 1978; Scott 1978; Evans and Conner 1979; Mannan et al. 1980). These studies show that many vertebrates regularly use snags for nesting, feeding, shelter, communication, and resting.

Early in this century, Grinnell and Storer (1924) suggested that removing snags was detrimental to woodpeckers. Recently, several studies have described the impact of snag removal on other cavity-nesting birds as well. Haapanen (1965) found

that cavity-nesting bird densities declined in managed forests in Finland, while the density of noncavity-nesters was unchanged. He attributed the decline of cavity-nesters to the loss of nest holes in snags. Nilsson (1979) found that woodpeckers comprised a greater proportion of the breeding avifauna in unmanaged forests than in managed forests in southern Sweden. In Arizona, Balda (1975*b*) compared bird populations on a plot where snags were left standing to one with all pine snags removed. Secondary cavity-nesters (nonexcavators nesting in abandoned woodpecker holes or natural cavities) were 22% less abundant on the plot without snags. In a similar Arizona study, Scott (1979) compared bird densities before and after timber harvest on 2 plots, one with snags retained and one with snags cut. Cavity-nesting birds declined by 52% on the snag removal plot and increased by 23% on the plot with snags. Cavity-nesters on a third, uncut control plot increased by 31% during the same time period. In a Sierra Nevada study, Beaver (1972) compared brush fields with and without snags and found 30% more bird species (all cavity-nesters) on the plot with snags.

Many species of forest wildlife depend upon snags. Recent federal laws, particularly the Multiple-Use Sustained Yield Act, Endangered Species Act, National Environmental Policy Act, and National Forest Management Act, require land managers to include wildlife needs in forest planning and management. Land managers need more information about how wildlife species use snags, about which species are dependent upon snags, about the characteristics of snags that are useful to different species of wildlife, and about the numbers of snags that are needed to support various densities of wildlife populations. Gale's (1973) survey is, to our knowledge, the only published study of snags used for nesting and feeding in California.

The objectives of our study were (1) to describe the characteristics of sites used for nesting and feeding by cavity-nesting bird species, (2) to assess the importance

of snags for nesting and feeding, (3) to describe patterns of snag deterioration by tree species and size, (4) to describe relationships between abundance and structural characteristics of snags and cavity-nesting bird populations, and (5) to suggest management guidelines for conifer forests of the Sierra Nevada.

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## THE STUDY AREA

All field work was conducted within a 20-km radius of the University of California Sagehen Creek Field Station. The station is located on the east side of the Sierra Nevada, 13 km north and 6 km west of Truckee, California, at latitude 39°26'N and longitude 120°14'W (Fig. 1). Elevations vary from 1,880 to 2,670 m. Field work was concentrated within the upper Sagehen Creek drainage, an area of 39

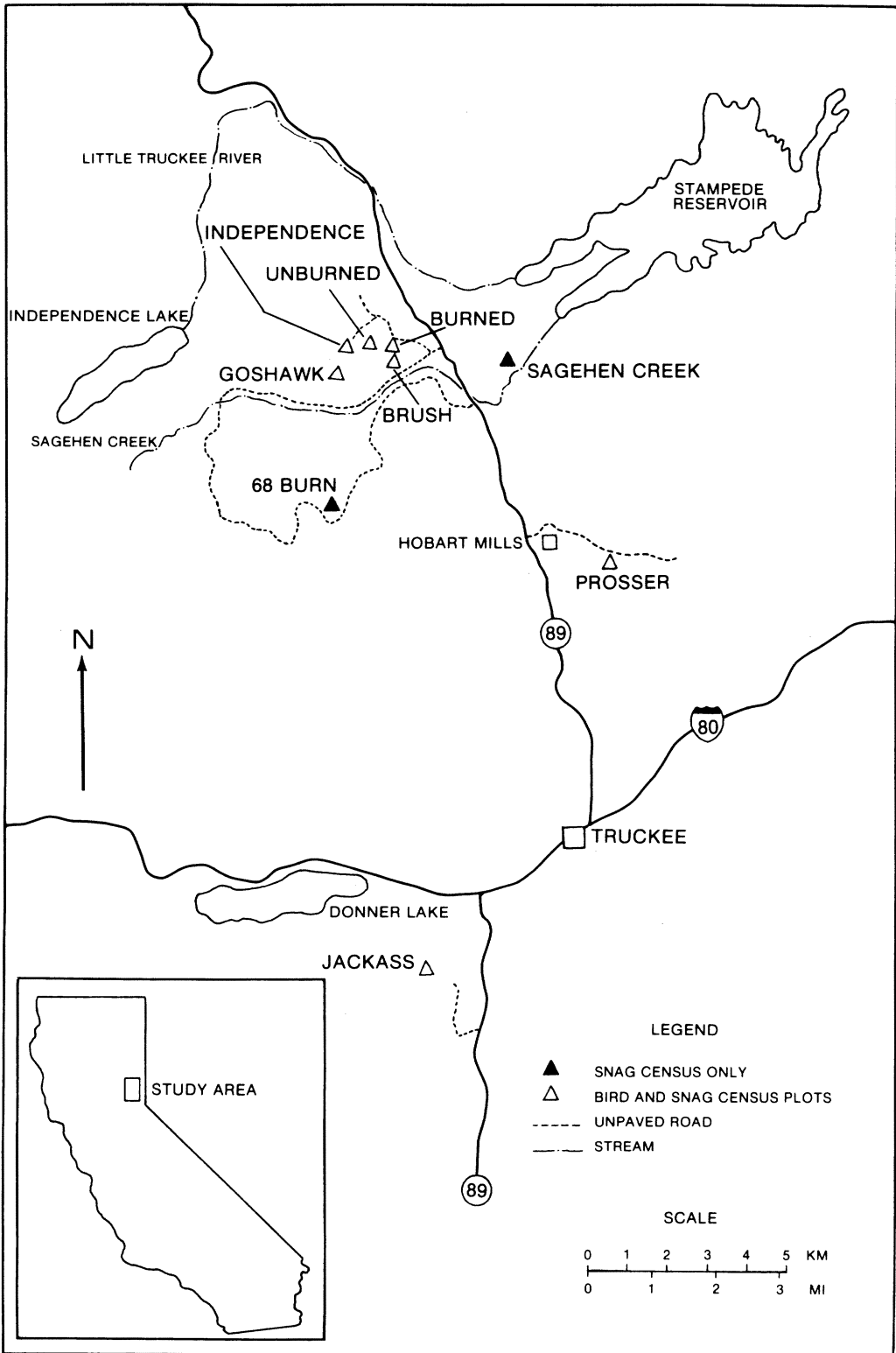


Fig. 1. Location of study area and census plots.

km<sup>2</sup>. The basin was dominated by a second-growth forest of Jeffrey pine (all scientific names appear in the Appendix) and white fir, and by brush fields or conifer plantations on the site of the 1960 Donner Ridge fire that burned approximately 16,000 ha, including the eastern quarter of the basin. Meadows, lodgepole pine, and aspen occur in wet areas near springs and streams, and red fir and mountain hemlock dominate at higher elevations. Stands of Jeffrey pine with a sagebrush understory are found at lower elevations along the eastern edge of the basin.

Winters at Sagehen Creek are long and cold, and summers are warm and dry. Average monthly maximum temperatures for the period 1954–78 at the Sagehen Creek Station ranged from 4 C in December and January to 27 C in July. Average monthly minimum temperatures for this period ranged from –11 C in December and January to 2 C in July. Mean monthly precipitation for the 1954–78 period varied from 1 to 18 cm, most occurring as snow from November through April.

## METHODS

### Study Plots

We selected 9 major plots to study birds and/or snags (Fig. 1). On 7 plots we studied both birds and snags. The Unburned and Goshawk plots were chosen to represent old-growth pine–fir, the Independence and Jackass plots represented logged pine–fir, the Burned and Brush plots were in burned pine–fir, and the Prosser plot was in the pine–sage type. On 2 major plots we measured only snags. The 1968 Burn plot was in burned red fir type, and the Sagehen plot was in a riparian area.

All plots occurred at similar elevations, 1,800–1,950 m, and were located on nearly level terrain along broad ridge tops. Each plot measured 214 × 397 m and covered 8.5 ha, excepting the Brush plot, which was only 6.7 ha and measured 183 × 366 m. Each plot was marked with plastic flagging at 30.5-m intervals. The intervals were numbered consecutively,

and the grids were walked during bird censuses and were used to plot the location of birds on field maps.

### Vegetation Measurements

Plant species composition and cover were estimated on each study plot using a point-intercept method (Mueller-Dombois and Ellenberg 1974). Presence of plant species, bare ground, logs and rocks, and litter was recorded at 1-m intervals along 3 equidistant transects running the length of a plot. A plant species was recorded as present at a point if it was intercepted by a line projected vertically above or below a horizontal measuring tape, but bare ground, litter, and logs or rocks were counted only if no vegetation was present.

Live tree basal area and density were estimated on each plot using the point-centered quadrat technique of Cottam and Curtis (1956) as specified by Mueller-Dombois and Ellenberg (1974). Sample points were located at every other 30.5-m grid intersection. Only trees >1.5 m tall were counted.

Foliage height diversity was estimated by the MacArthur and Horn (1969) technique. Ten 30.5-m lines were run in random directions from points evenly distributed over the plots. A tripod-mounted 35-mm camera with a 200-mm lens was aimed vertically over 10 random points along each line, and any foliage intercepts at each of 16 points on the camera view finder were recorded as well as the foliage height at each point. Foliage intercepts lower than the minimum focusing range of the camera (2.0 m above the lens, 3.5 m above the ground) were measured directly using a tape measure held vertically along a plumb line. Foliage height diversity was computed with the Shannon–Wiener formula (Shannon and Weaver 1949) using height intervals of 60, 60–750, and >750 cm following Beaver (1972).

### Snag Measurements

All snags on each study plot >1.5 m tall and >13 cm dbh were marked with num-



bered metal tags and entered on plot maps. For each snag we recorded species, dbh, height (measured directly with a tape or estimated with an Abney level or Relaskop), number of limbs >1 m long, limb condition (presence of main branch, secondary branches, or foliage-bearing twigs), percent of bark remaining on the stem, and presence of needles, top, nest-cavities, and feeding sign (feeding excavations).

For cavities in snags on the plots we recorded hole height, snag diameter at hole height (DHH), hole dimensions, cavity depth, cavity diameter, sill width (distance from outer surface to point where cavity turns downward), and species using hole, if known. Not all holes were safely accessible using ladders or climbing spikes; for these cavities hole height and DHH were estimated using a Relaskop, and the other cavity measurements were omitted. Cavity starts (i.e., incompletely excavated cavities) were excluded from all analyses.

### Nest Site Characteristics

We searched for active nesting cavities throughout the Sagehen Creek basin in 1976, 1977, and 1978. Active nests were confirmed by observing adults enter the cavity to feed young or incubate eggs, or by the sounds of young calling from the nest. Confirmed nest sites were marked and plotted on maps for measurement after the nesting period.

Nest trees were photographed and measured in the manner described above for snags. Additionally, we recorded the condition of the tree as dead, live with dead top, live with dead portion of bole, live tree, stump (<1.5 m tall), log, or other. All accessible cavities were also measured as described above.

We sampled the characteristics of the habitat surrounding a nest site using a 0.04-ha, circular plot (11.3 m radius) centered at the nest. On each plot, we recorded forest type (subjectively classified as burned pine-fir, burned red fir, burned pine-fir edge or burned red fir edge if located within 20 m of burn border, pine-

fir, red fir, lodgepole, lodgepole-meadow, open pine, pine-sage, or aspen), maximum canopy height (measured using a Relaskop), canopy cover (estimated foliage cover of trees >8 cm dbh), shrub cover (estimated percent of ground covered by woody perennials including trees ≤8 cm dbh), and number of live and dead stems by size classes (assigned using a Biltmore stick to classes of >8–15, >15–23, >23–38, >38–53, >53–69, >69–84, >84–102, and >102 cm dbh [James and Shugart 1970]).

Because nests might have been easier to detect in open burns or in meadows, we recorded the distances (measured by pacing) at which we initially detected nests in 1978 in meadow, forest, and burn habitats. Nests of 4 bird species were numerous enough to perform a 2-way analysis of variance (ANOVA) comparing mean detection distances among birds and habitat types.

### Random Plots

To describe the habitats available to birds for the analysis of habitat selection, we located a random sample of 100 0.04-ha, circular plots throughout the Sagehen Creek basin and made the same measurements as on the nest plots. We used 100 plots so that mean live tree basal area could be estimated to within ±10%, based on the variance calculated from a preliminary sample (Dilworth 1973:218).

This sample was drawn using a 2-stage design. On an enlarged topographic map of the basin, we numbered consecutively each of the 23 square-mile sections. We then constructed a transparent 100-point grid to fit within a section outline. For each plot, we chose a section using a random number table, and then randomly chose a grid point within that section.

Each point was marked on the topographic map and later transferred to an aerial photo of the basin. We located plot centers on the ground using compass direction and distance from each point to the nearest road or neighboring point.

## Foraging Observations

We used 2 approaches in estimating the importance and measuring the characteristics of snags used for foraging. First, we noted the presence of foraging sign (chipped bark or excavation into sapwood) on all snags located on the study plots. These data allowed a comparison of characteristics of trees used for feeding with characteristics of those not used, but this comparison did not take into consideration trees used as feeding substrates by bark-gleaning or flycatching birds.

To make a more complete comparison of foraging behavior among species, we followed individual birds and described their behavior into a portable tape recorder. Observations were limited to primary cavity-nesting species (all excavators except northern flicker, a ground-forager) and bark-gleaning nonexcavators. We recorded bird species, substrate (live tree, snag, log, brush, ground, or air), position on tree (trunk, branch, foliage), tree species, diameter and height, foraging height, and foraging method (glean, drill, sapsuck, flycatch). Timing was continued until a bird flew to a new tree, shifted to a new position or branch within a tree, changed its foraging height on the tree by more than 1 m, or changed its foraging method. No more than 5 such sequential activities were recorded for any bird during an observation period. After observations were terminated, we replayed the tape and used a stopwatch to time each foraging bout.

## Avian Population Trends

Breeding bird populations were censused on all plots using the spot-map technique (Williams 1936) as applied by Bock and Lynch (1970). The relative merits of the technique were discussed by Robbins (1978) and Ralph and Scott (1981).

Censuses were conducted from May to early July, usually from 0600 to 1100 hours. Occasional censuses were conducted in the late afternoon. Each census last-

ed 2–4 hours. On each visit, censuses were begun at alternate sides of the plot, and observers were rotated. Each plot was censused from 10–16 times/year.

## Data Analysis

Our analysis of nesting and foraging habitat use followed 2 main approaches: (1) we compared habitat characteristics between a species (or a pooled group of species) and our sample of random plots to evaluate evidence of nonrandom selection of habitats, and (2) we compared the characteristics of habitats among species to highlight interspecific similarities and differences. To test for evidence of nonrandom selection of categorical habitat characteristics (e.g., forest types, tree species, tree diameter class), we computed the proportion of each category used by a species and compared this proportion to the proportion available in that type. The difference between these proportions (use minus availability) was used as a preference index. Confidence intervals around these index values were computed using the formula described by Strauss (1979). Index values range from  $-1.0$  (complete avoidance) to  $1.0$  (exclusive use). Values statistically different than 0 indicated nonrandom habitat use, but cannot be used to assume an actual “preference” of a species for a habitat category. One must always be aware that the magnitude of these values is highly dependent on the number of categories that were originally defined for analysis.

Niche breadth and overlap in distribution of nests among forest types, and foraging behavior and habitat use, were calculated using the Colwell and Futuyma (1971) method. Unless noted otherwise, equations (21) and (24) of Colwell and Futuyma (1971) were used to calculate niche breadth and overlap, respectively. This method applies a weighting factor to each resource state (habitat category) based on the distinctness of that state as estimated from the pooled abundance of all species in the analysis (see Colwell and

Futuyma 1971 and Inger and Colwell 1977 for a complete discussion of methods). The program COFU, written by R. K. Colwell, was used for all computations (Duncan and Phillips 1980).

Discriminant analyses of nest and foraging site characteristics were computed using the SPSS program package (version 8.0, Nie et al. 1975). Stepwise analyses were performed using Wilk's method (Klecka 1975). In multigroup analyses, the number of possible functions derived is the lesser of either 1 less than the number of groups (in this case, species) or the number of variables in the analysis. In this study, we report only those functions that explained at least 5% of the total variance.

To interpret the biological meaning of each discriminant function, we calculated the pooled within-species correlation of each variable with the discriminant score derived for each function (structure matrix). Variables with the highest correlations were then used to identify each function. Some authors (e.g., Klecka 1975) have recommended interpreting functions using the magnitude of the standardized discriminant function coefficients (pattern matrix), but these coefficients are subject to greater variability than the correlations (Marascuilo and Levin 1982).

Cluster analyses (UPGMA, Sneath and Sokal 1973) were used to study similarities of nesting and foraging habitat use among bird species. These analyses were based on matrices of either niche overlap values or Euclidian distances between mean discriminant scores of each species-pair. Raphael (1981) discussed the advantages of Euclidian distance as a measure of species similarity in discriminant analyses (cf. Harner and Whitmore 1977). The program CLUST, written by W. W. Moss (Duncan and Phillips 1980) was used to construct dendrograms from the overlap or Euclidian distance cluster analyses.

## RESULTS AND DISCUSSION

### Nest Stand Characteristics

*Forest Types.*—We found 561 active cavity nests occupied by 18 bird species

Table 1. Cavity-nesting bird species breeding in the Sagehen Creek study area, common name codes, and number of active cavity nests observed in this study.

Classification and species	Code name	Number of active cavity nests
Excavators <sup>a</sup>		
Northern flicker <sup>b</sup>	NF	68
Lewis' woodpecker	LW	37
Red-breasted sapsucker	RS	49
Williamson's sapsucker	WS	50
Hairy woodpecker	HW	19
White-headed woodpecker	WW	11
Black-backed woodpecker	BW	7
Red-breasted nuthatch	RN	30
Pygmy nuthatch	PN	28
Nonexcavators <sup>c</sup>		
American kestrel	AK	13
Tree swallow	TS	14
Mountain chickadee	MC	131
White-breasted nuthatch	WN	25
Brown creeper	BC	17
House wren	HR	21
Western bluebird	WB	2
Mountain bluebird	MB	37
European starling	ES	2
Total		561

<sup>a</sup> Species that excavate their own nest cavities. RN and PN occasionally use existing holes.

<sup>b</sup> Scientific names appear in Appendix.

<sup>c</sup> Species nesting in existing cavities. MC and WN occasionally excavate their own cavities.

(Table 1). Most of these nests were in burned pine–fir forest (33%) or in lodgepole–meadow (24%). These 2 habitat types were selected for nesting in significantly greater proportion (binomial test,  $P < 0.05$ ) than they occurred in the Sagehen Creek basin. In contrast, pine–fir, pine plantation, and red fir habitat types had significantly fewer nests than expected if nests had been distributed randomly among habitat types (Fig. 2).

These differences in nest site location apparently represented habitat preferences of the birds and were not biased because it might have been easier to detect an active nest in the more open habitats. Mean nest detection distance did differ among bird species, largely because of the long detection distance of the northern flicker. However, there was no significant difference in mean detection distance of any bird among meadow, forest, or burn habitats (Table 2).

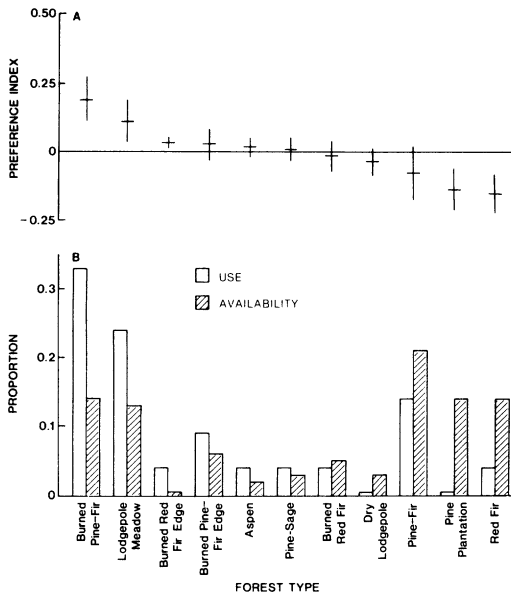


Fig. 2. Forest types used for nesting by cavity-nesting birds. A = preference index (use minus availability). Vertical lines indicate 95% confidence interval of index value (Strauss 1979). B = proportions used and available.

Species diversity ( $H'$ , the Shannon-Wiener index), a measure of the number of species and relative abundance of birds nesting in each habitat type, was highest in burned pine-fir edge, burned pine-fir, and in lodgepole-meadow. It was lowest in pine plantations and in dry lodgepole types (Table 3). According to relative niche breadth (Colwell and Futuyma 1971), an index of the variety of habitats used by individual bird species, the mountain chickadee used the widest variety of

types, and the black-backed woodpecker, Lewis' woodpecker, American kestrel, and the brown creeper nested in the most restricted range of habitat types (Table 3).

To measure the degree to which each bird species nested randomly in available forest types, we computed overlap values (Colwell and Futuyma 1971) between each species' use of forest types and distribution of those types within our random sample of plots. A value of 1.00 indicated complete overlap (i.e., random selection) and 0.00 indicated no overlap (maximum selectivity). According to this measure, the distribution of nests of mountain chickadee, Williamson's sapsucker, and white-breasted nuthatch overlapped most with the frequency of occurrence of these different habitat types in the 100 random plots. These species were the least selective. The smallest degree of overlap occurred in the distribution of nests of the black-backed woodpecker and American kestrel. These species were the most selective. These overlap values were highly correlated with the niche breadth values (Spearman rank correlation,  $r = 0.95$ ,  $P = 0.001$ ). Thus, either measure served as an index of habitat selectivity.

We also computed habitat overlap values between each pair of species (except starling and western bluebird). These values (Raphael 1980:30) were then used in a UPGMA cluster analysis to construct a dendrogram to examine affinities among species (Fig. 3). This dendrogram illustrated 3 groups of species at the 0.75

Table 2. Analysis of variance of nest detection distance (m) differences among birds and habitat types.

Source of variation	N	Mean distance	F	P
Habitat type			1.27	0.207
Meadow	46	39		
Forest	26	38		
Burn	33	67		
Bird			11.21	0.001
Mountain chickadee	37	25		
Northern flicker	25	104		
Williamson's sapsucker	23	30		
Red-breasted sapsucker	20	39		
Interaction			0.54	0.775

Table 3. Percent of random plots and percent of nests occurring in each forest type in the Sagehen Creek basin.

Forest type	Random plots	Bird species <sup>a</sup>					
		AK	MC	BC	MB	HR	PN
Pine-sage	3	15	8	0	3	5	4
Pine-fir	21	0	18	29	0	0	7
Burned pine-fir	14	69	25	0	70	38	79
Pine plantation	14	0	0	0	0	0	0
Burned pine-fir edge	6	15	8	12	5	14	11
Lodgepole-meadow	13	0	25	53	5	29	0
Dry lodgepole	3	0	1	0	0	0	0
Aspen	2	0	3	0	0	0	0
Red fir	19	0	4	0	0	0	0
Burned red fir	5	0	4	0	11	14	0
Burned red fir edge	0	0	4	6	5	0	0
Relative niche breadth		0.33	0.78	0.33	0.39	0.52	0.36
Relative overlap with random plot distribution		0.56	0.92	0.62	0.63	0.72	0.65
Sample size	100	13	131	17	37	21	28

<sup>a</sup> See Table 1 for bird name codes.

overlap level: burn specialists, forest specialists, and habitat generalists. The black-backed woodpecker and white-headed woodpecker were not aligned with any of these categories and appeared unique in their habitat use patterns. However, these 2 species were represented by only 7 and 11 nests, respectively, and apparent dissimilarity to other species may have been an artifact of small sample size.

*Forest Stand Structure.*—We used stepwise discriminant analysis to test for differences in surrounding stand structure among nest sites of each excavator species. This analysis, based on 7 variables (Table 4) compared among 8 bird species, resulted in 2 significant discriminant functions. The first explained 52% of the total variation and was most highly correlated with canopy height, live tree basal area, and whether the forest was burned (Table 5). These variables were related: burned forests had both low canopy height and low live tree basal area. The second function explained only 7% of the total variation and was correlated with shrub cover and, to a lesser degree, live tree basal area and the number of snags >38 cm dbh/ha. The bird species were aligned along these 2 discriminant axes in 2 groups (Fig. 4): 3 species nesting in unburned tall-canopy forest and 6 species nesting in burned for-

est. The variables that best discriminated among bird species were those with the highest univariate *F* ratios and earliest entry step (Table 4). These were the same variables that were most correlated with the discriminant scores (Table 5): canopy height, basal area of live trees, burned vs. unburned forest, and shrub cover. These appear to be the forest stand attributes that differ most among nests of these birds.

*Comparisons with Random Plots.*—It is also important to examine whether nest site characteristics differ from the same characteristics measured on the randomly sampled plots. First, we pooled all excavator nests to compare stand characteristics between all nest sites and the random plots using a 2-group discriminant analysis. Among the 7 stand variables, the greatest difference between nests and random plots occurred in the density of large snags (Table 4). As a group, nest plots of excavators did not differ from the random plots in proportions of burned or unburned forest or in average canopy height (Table 4). Although the discriminant function showed a significant difference between nest plots and random plots, the distinction was rather weak; only 13% of the total variance was explained. The discriminant function correctly classified 67% of all plots. Fewer nest plots were cor-

Table 3. Continued.

RN	TS	WN	BW	HW	Bird species						ES	Bird species diversity ( $H'$ )
					NF	LW	WW	WS	RS	WB		
3	7	0	0	0	4	0	18	2	0	0	0	1.87
53	0	36	0	11	6	0	0	18	16	0	0	1.92
3	29	40	0	26	41	87	18	4	4	100	0	2.22
0	0	0	0	0	0	3	0	0	0	0	0	0.00
7	0	4	14	11	7	3	9	18	8	0	0	2.40
27	64	8	29	32	28	8	0	34	37	0	100	2.22
0	0	0	0	0	0	0	0	0	2	0	0	0.69
3	0	8	0	0	3	0	0	6	16	0	0	1.58
0	0	0	29	0	0	0	18	16	6	0	0	1.46
3	0	4	29	11	6	0	18	0	0	0	0	2.07
0	0	0	0	11	4	0	18	2	10	0	0	1.92
0.43	0.41	0.61	0.32	0.68	0.62	0.32	0.59	0.62	0.61	0	0	
0.77	0.65	0.87	0.52	0.83	0.81	0.60	0.67	0.87	0.82	0	0	
30	14	25	7	19	68	37	11	50	49	2	2	

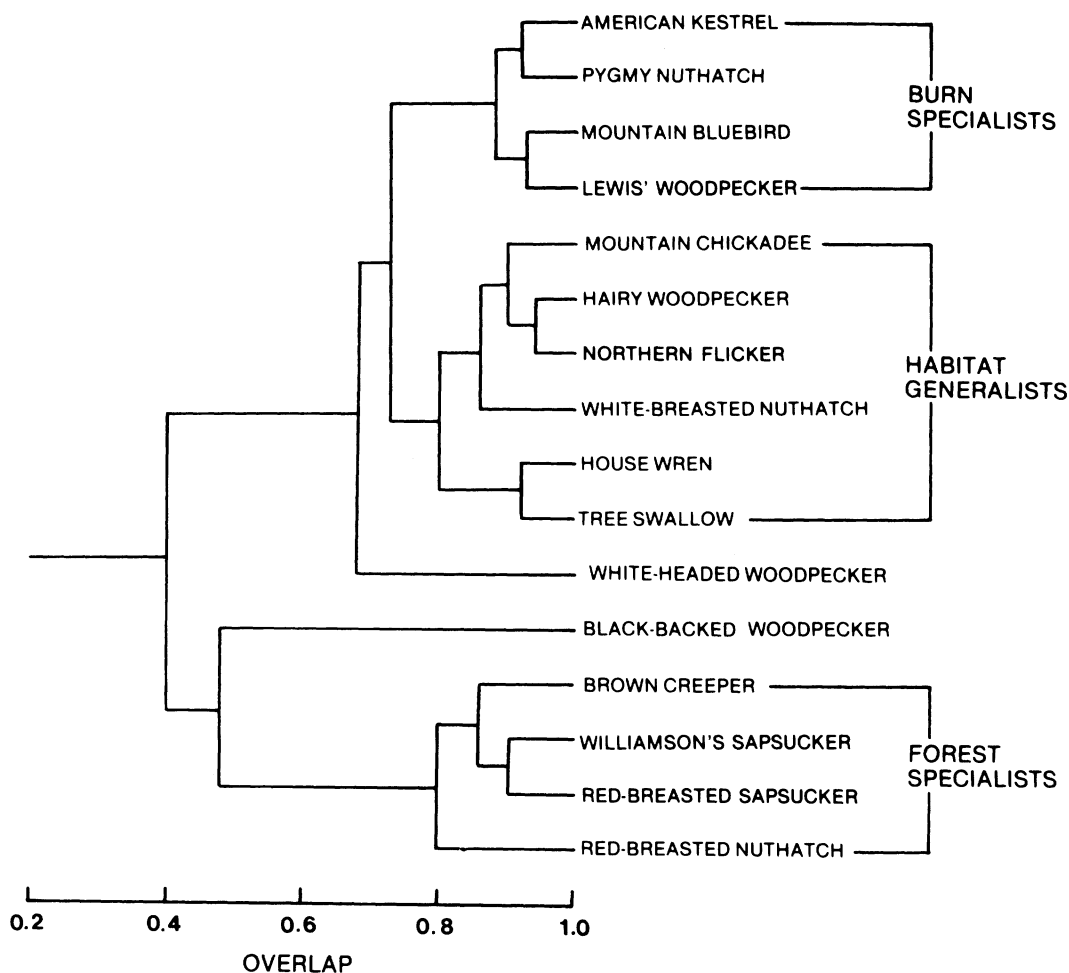


Fig. 3. Dendrogram showing interspecific overlap of the distributions of bird nests among forest types. Maximum overlap (1.0) indicates maximum similarity.

Table 4. Discriminant analyses comparing stand characteristics among nest sites of each excavator and comparing excavator nest sites as a group to the random plots.

Variable	Means		Univariate <i>F</i> ratio <sup>a</sup>		Step entered <sup>b</sup>		Significance as discriminator <sup>c</sup>	
	Nest sites <i>N</i> = 299	Random plots <i>N</i> = 100	Among spp.	Nest plots vs. random plots	Among spp.	Nest plots vs. random plots	Among spp.	Nest plots vs. random plots
Burned or unburned	0.49	0.39	15.99**	3.12	3	6	0.000	0.110
Shrub cover (%)	0.29	0.39	4.79**	5.96*	4	3	0.033	0.001
Canopy height	13.7	15.1	30.53**	1.07	1	5	0.000	0.041
Snags ≤23 cm/ha	34.4	16.0	1.33	6.23*	6	7	0.120	0.292
Snags >23–38 cm/ha	22.1	5.7	2.21*	17.77**	5	2	0.073	0.005
Snags >38 cm/ha	18.4	4.7	1.45	22.09**	7	1	0.638	0.000
Basal area live trees (m <sup>2</sup> /ha)	17.1	23.8	23.59**	6.46*	2	4	0.000	0.001

<sup>a</sup> Univariate tests performed prior to discriminant analyses.  
<sup>b</sup> Order in which variable entered discriminant equation. Variables entered first are best discriminators.  
<sup>c</sup> Probability that variable does not contribute to the discrimination among groups given variables already entered. Measured using change in Rao's *V* (Klecka 1975).  
\* *P* < 0.05.  
\*\* *P* < 0.01.

rectly classified (65%) than were random plots (73%).

Second, we compared nest plots of each excavator with our random plots using a separate 2-group discriminant analysis for each species. All comparisons resulted in significant discriminant functions, indicating that nest stand characteristics of each excavator differed from characteristics that would be expected if birds located their nests randomly with respect to habitat. Classification success is an index of similarity between nest sites and random plots; the larger the percentage cor-

rect, the less overlap. These values ranged from 65% for Williamson's sapsucker to 91% for white-headed woodpecker (Table 6).

Variables that were most consistently significant as discriminators were snags >38 cm and shrub cover. As measured by its correlation with the discriminant scores, the number of snags >38 cm was the variable most strongly identified with the discriminant functions. Apparently, excavators selected nests surrounded by large snags.

Nest Tree Characteristics

*Condition.*—We found 72% of the nests in snags and 19% in dead tops of live trees (Table 7). Six percent of the nests were in logs or stumps. Live trees held only 2% of the total nests. Snags contained the majority of nests of all species except for the 2 species of sapsuckers that nested most often in the dead tops of live trees.

The proportion of snags used for nesting was much higher than expected based on counts of all live trees and snags on our randomly sampled plots. Only 7% of the available trees were snags, but 72% of those used for nesting were snags. Thus, snags were highly preferred as nest sites.

Table 5. Correlations of variables describing stand characteristics with discriminant scores (structure matrix). Analysis based on 299 excavator nest sites.

Variable	Discriminant function	
	I	II
Burned or unburned	−0.76	−0.10
Shrub cover (%) <sup>a</sup>	−0.38	0.67
Canopy height	0.93	0.07
Snags ≤23 cm/ha	0.03	−0.13
Snags >23–38 cm/ha	−0.21	0.06
Snags >38 cm/ha	−0.22	−0.28
Basal area live trees (m <sup>2</sup> /ha)	0.86	−0.34

<sup>a</sup> Arcsine transformed.

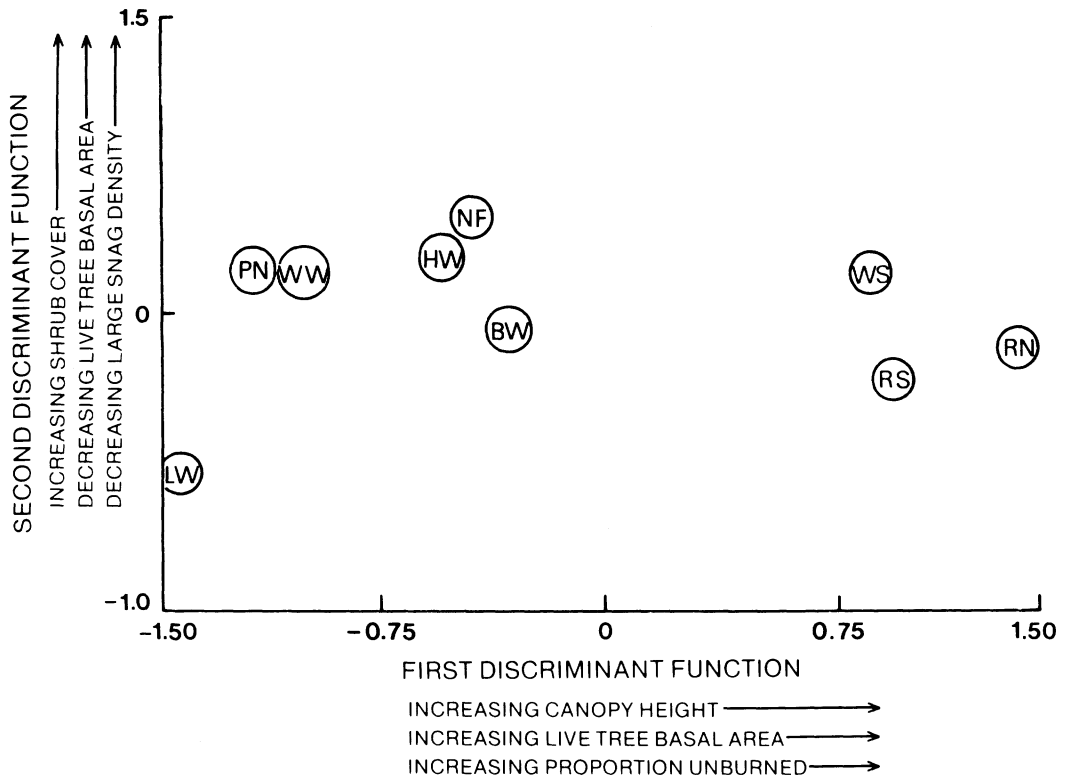


Fig. 4. Mean scores of excavators on first 2 axes derived from discriminant analysis of nest stand characteristics. See Table 1 for bird name codes.

*Species.*—We found cavity nests in 9 species of trees (Table 8). White fir was selected for nesting in much greater proportion than it occurred in the Sagehen Creek basin. Jeffrey pine and lodgepole pine were used in proportion to availability, and red fir was used less than expected. Incense-cedar, sugar pine, and western white pine were used only rarely (18 nests, total) and were pooled in an “other” group along with nests in power poles and other nontree locations. The house wren, Williamson’s sapsucker, and northern flicker nested in the greatest diversity of tree species, and the American kestrel, tree swallow, and Lewis’ woodpecker used the lowest diversity (Table 8).

These differences among bird species might have reflected tree species availability in the forest types selected by the birds. To clarify the patterns of snag

species use and availability, we plotted percent bird use against percent availability for 4 snag species (Fig. 5). We computed availability separately for each bird species based on the proportions of forest types used by each. We used these proportions to create weighted snag species frequencies in each type and then compared these totals to the observed distribution of nests. White fir snags clearly were favored by more bird species than any other snags (Fig. 5). Only 2 birds favored Jeffrey pine or lodgepole pine snags, but 8 birds favored these species when nests in both live and dead trees were counted (Table 8). Apparently, Jeffrey pine and lodgepole pine were more suitable as nest sites when alive.

*Decay State.*—After a conifer dies, the snag undergoes a continual progressive degradation. Needles usually fall within 3



Table 6. Results of 2-group discriminant analyses comparing stand characteristics of excavator nest sites to a sample of 100 random plots.<sup>a</sup>

Variable	Excavator species <sup>b</sup>								
	PN	RN	BW	HW	NF	LW	WW	WS	RS
Burned vs. unburned	0.000	0.708	0.718	0.336	0.128	0.000	0.359	0.015	0.407
Shrub cover (%)	0.006	0.732	0.100	0.031	0.009	0.000	0.024	0.022	0.000
Canopy height	0.225	0.000	0.792	0.837	0.158	0.000	0.000	0.000	0.019
Snags ≤23 cm/ha	0.075	0.002	0.442	0.903	0.415	0.870	0.033	0.711	0.823
Snags >23–38 cm/ha	0.001	0.851	0.210	0.000	0.008	0.033	0.013	0.658	0.000
Snags >38 cm/ha	0.000	0.273	0.008	0.002	0.000	0.000	0.000	0.001	0.144
Basal area live trees (m <sup>2</sup> /ha)	0.010	0.745	0.031	0.010	0.000	0.348	0.348	0.000	0.516
Total correctly classified (%) <sup>c</sup>	84	72	87	82	73	87	91	65	70
Explained variance (%)	37	16	14	28	24	50	33	26	22
Sample size	28	30	7	19	68	37	11	50	49

<sup>a</sup> Values listed are probabilities that each variable does not contribute to the discrimination between nest sites and random plots. Lower values indicate better discriminators, tested using Rao's V (Klecka 1975).  
<sup>b</sup> See Table 1 for bird name codes.  
<sup>c</sup> Percentage of nests and random plots correctly identified using discriminant equations to classify each. This value is a measure of similarity between nest sites and random plots; larger values indicate lower similarity.

years (Keen 1955, Embry 1963), most needle-bearing twigs fall within 5 years (Scott 1978), and by 6 years snags lose tops and larger branches, and sapwood and heartwood decay (Scott 1978, Cline et al. 1980). We defined 6 decay states based upon external appearance (Table 9), similar to those described by Maser et al. (1979) and Cline et al. (1980). In our study, nesting frequency approximately doubled at each successively more decayed state. We found the largest proportion of nests (45%) in the most decayed snags (stage 6). Decay states 2–4 represented hard snags. Categories 5 and 6 were soft snags; most of these had been dead longer than 6 years.

We computed the percentage of snags available in each decay state for comparison (Table 9). These proportions corresponded closely to the pattern of nesting use, although snags in class 2 were used significantly less than their predicted frequency. Either birds were indiscriminant in their use of tree decay states for nesting, or these totals masked nonrandom selection by individual species.

To examine these 2 alternatives, we computed the differences between proportion of nest trees used and proportion available in each decay state for each bird species. There were marked interspecific differences in use of decay states among birds (Fig. 6). Mountain chickadees, white-headed woodpeckers, white-breasted nuthatches, and tree swallows used snags in decay state 6 more than expected. Snags in decay state 5 were used more than expected by American kestrel, mountain bluebird, pygmy nuthatch, hairy woodpecker, and Lewis' woodpecker; brown creeper, red-breasted nuthatch, black-backed woodpecker, northern flicker, Williamson's sapsucker, and red-breasted sapsucker used more snags in decay state 3 than occurrence suggested.

We used cluster analysis (Dixon and Brown 1977) to delineate groups of species using nest trees in similar decay states. For this analysis, we computed distance based on Phi-square (a measure of association) between each possible pair of species. A dendrogram based on this distance matrix

Table 7. Frequency of selection (%) as nest sites of various tree types by cavity-nesting birds at Sagehen Creek.

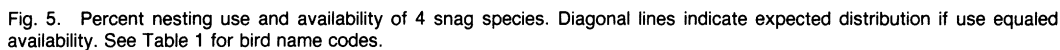
Bird species	Snag	Tree condition					Sample size
		Dead portion of live tree	Live tree	Stump <sup>a</sup>	Log	Other	
American kestrel	85	15	0	0	0	0	13
Mountain chickadee	58	12	4	15	9	2	131
Brown creeper	65	24	12	0	0	0	17
Mountain bluebird	95	3	0	0	3	0	37
House wren	85	0	0	10	0	5	21
Pygmy nuthatch	100	0	0	0	0	0	28
Red-breasted nuthatch	73	27	0	0	0	0	30
Tree swallow	100	0	0	0	0	0	14
White-breasted nuthatch	80	20	0	0	0	0	25
Black-backed woodpecker	71	29	0	0	0	0	7
Hairy woodpecker	84	16	0	0	0	0	19
Northern flicker	78	20	2	0	0	0	68
Lewis' woodpecker	100	0	0	0	0	0	37
White-headed woodpecker	82	0	0	9	9	0	11
Williamson's sapsucker	40	58	2	0	0	0	50
Red-breasted sapsucker	47	47	6	0	0	0	49
Western bluebird	100	0	0	0	0	0	2
European starling	100	0	0	0	0	0	2
All nests	72	19	2	4	2	1	561

<sup>a</sup> Snags <1.5 m tall.

Table 8. Percentages of nests found in various species of live trees and snags.

Bird	Jeffrey pine	Lodgepole pine	White fir	Red fir	Aspen	Other <sup>a</sup>	Diversity index (H')
American kestrel	31	0	69	0	0	0	0.62
Mountain chickadee	17	23	37	12	3	9	1.37
Brown creeper	29	53	6	6	0	6	1.20
Mountain bluebird	16	5	62	14	0	3	1.12
House wren	38	24	19	14	0	5	1.45
Pygmy nuthatch	28	0	64	7	0	0	0.83
Red-breasted nuthatch	13	23	47	13	0	3	1.13
Tree swallow	14	71	14	0	0	0	0.79
White-breasted nuthatch	28	4	60	0	8	0	0.99
Black-backed woodpecker	14	43	0	43	0	0	1.00
Hairy woodpecker	11	32	42	16	0	0	1.26
Northern flicker	21	25	43	7	3	0	1.41
Lewis' woodpecker	43	3	54	0	0	2	0.80
White-headed woodpecker	27	9	9	55	0	0	1.12
Williamson's sapsucker	12	36	30	18	1	2	1.45
Red-breasted sapsucker	0	29	49	12	10	0	1.19
Western bluebird	100	0	0	0	0	0	0.00
European starling	0	100	0	0	0	0	0.00
Total use (U)	19	23	41	12	2	3	
Availability (A)	19	23	29	20		9	
Preference index <sup>b</sup>	0.0	0.0	0.12*	-0.08*		-0.04*	

<sup>a</sup> Other includes sugar pine, incense-cedar, western hemlock, western white pine, unknown spp., and nests not in trees.<sup>b</sup> Preference = (U - A) ÷ 100 (Strauss 1979).\* Values significantly different than zero ( $P < 0.05$ , binomial test).



Decay state	Description of decay state				Condition of top		Percent nests in snags	Percent of available snags
	Condition of tree	Needles	Twigs	Branches	Intact	Broken		
1	live	present	present	most present	73	49		
2	dead	present	present	most present	10	5	3.6*	7.0
3	dead	absent	present	most present	21	12	7.9	10.6
4	dead	absent	absent	most present	35	32	16.1	16.6
5	dead	absent	absent	some present	13	103	27.8	23.6
6	dead	absent	absent	none present	1	185	44.6	42.3

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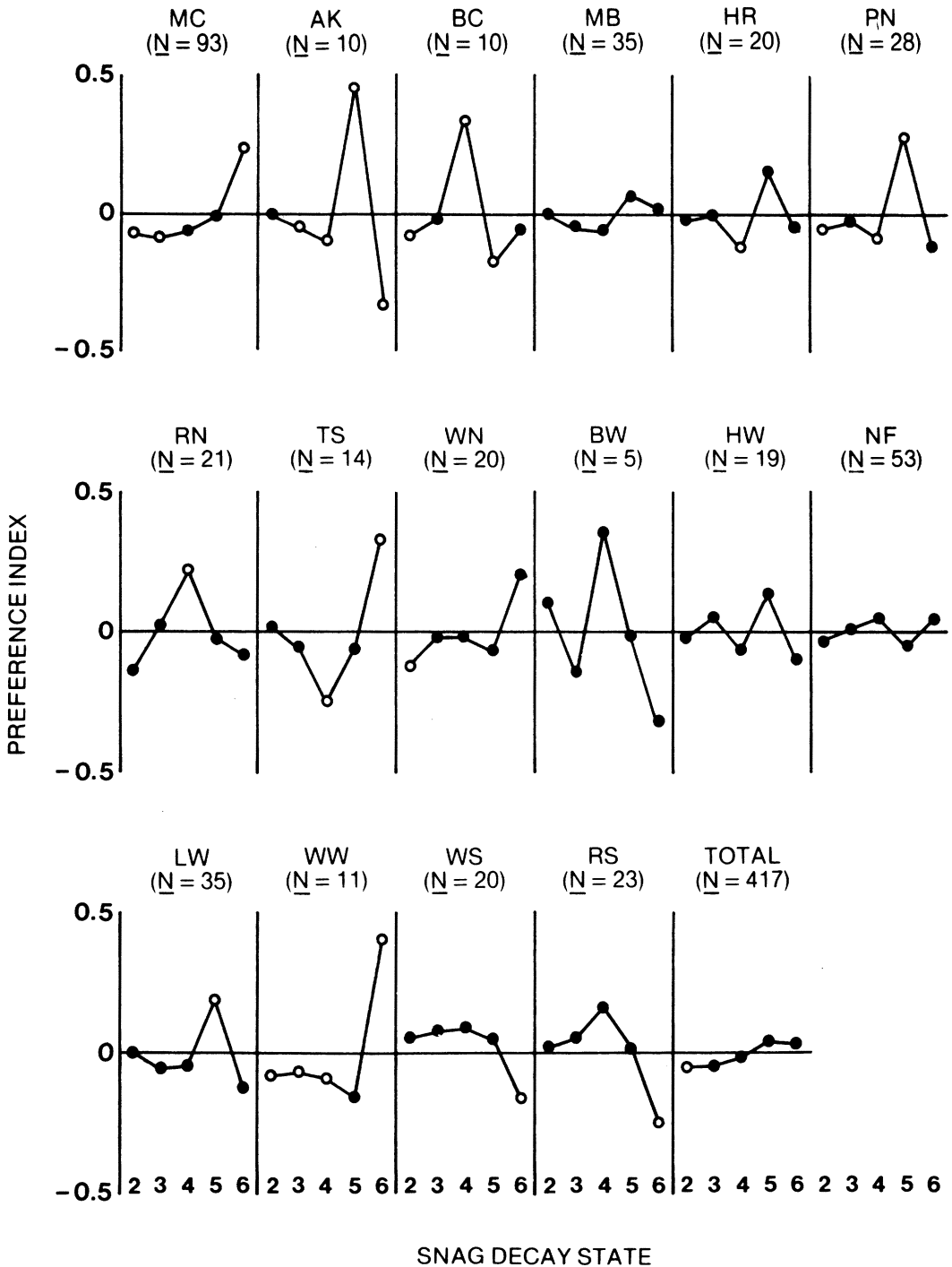


Fig. 6. Preference (use minus availability) of cavity-nesting birds for snag decay states (Table 9). Open circles indicate values statistically different from zero ( $P < 0.05$ , binomial test). See Table 1 for bird name codes.

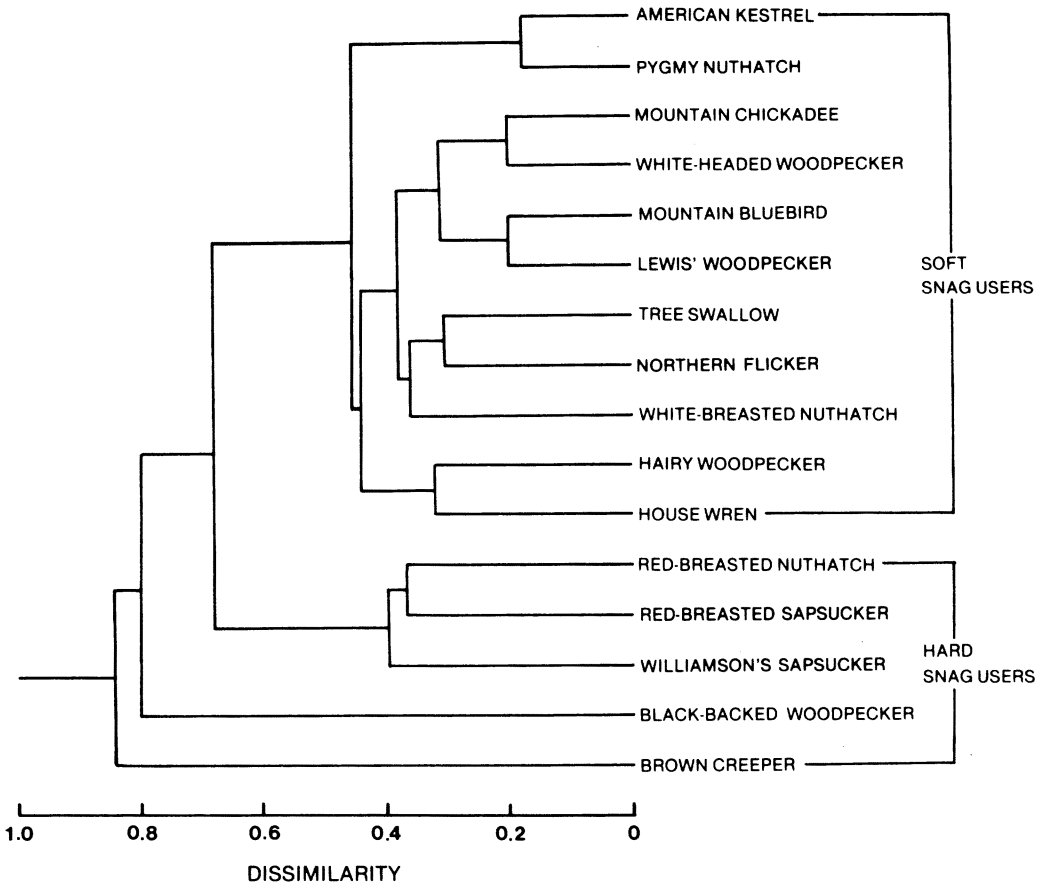


Fig. 7. Birds nesting in hard and soft snags, according to cluster analysis using number of nests in each snag decay state (Table 9).

revealed a hard-snag group and a soft-snag group (Fig. 7). Birds at the top of Figure 7 used the softest, or most decayed snags. Those at the bottom used the hardest trees. This trend was related to foraging habits of the birds, at least for excavators. Species feeding from the ground or air (northern flicker, Lewis' woodpecker) and surface gleaners (pygmy nuthatch, white-headed woodpecker) nested in soft snags. Those that drilled for food (black-backed woodpecker, red-breasted sapsucker, and Williamson's sapsucker) nested in harder snags. The hairy woodpecker, which drilled for prey but was grouped with soft-snag users, and the red-breasted nuthatch, which gleaned but nested in hard snags, were exceptions to the trends.

Bark retention is related to decay state and to time since tree death, but this relationship varies among tree species. Cline et al. (1980), for example, found that Douglas-fir snags in western Oregon lost 4% of their bark within 4 years, 50% within 8 years, and 71% by 17 years. Scott (1978), however, found that bark retention was not a good indicator of age of ponderosa pine snags in Arizona. The growth of wood decay fungi is most affected by moisture and temperature (Kimmey 1955). Bark insulates a snag and prevents drying. Snags with bark should decay faster than snags without. We expected, therefore, that bark cover would be greater on nest snags than on non-nest snags. Comparisons of snags with and

Table 10. Mean percentage of bark cover on nest snags of cavity-nesting birds in relation to hardness classification.

Bird species	Hardness classification <sup>a</sup>	Mean % bark cover
Black-backed woodpecker	H	20 A <sup>b</sup>
Tree swallow	S	25 A
House wren	S	35 A
Hairy woodpecker	S	37 A
White-headed woodpecker	S	41 AB
Mountain chickadee	S	54 AB
Brown creeper	H	56 ABC
Lewis' woodpecker	S	59 ABC
Pygmy nuthatch	S	62 ABC
Mountain bluebird	S	63 BC
Northern flicker	S	65 BC
White-breasted nuthatch	S	69 BC
Red-breasted sapsucker	H	69 C
Williamson's sapsucker	H	84 C
Red-breasted nuthatch	H	85 C
American kestrel	S	87 C

<sup>a</sup> Classification based on Fig. 7. H = Hard, S = Soft.<sup>b</sup> Means with the same letters are not significantly different ( $P > 0.05$ , Duncan's multiple range test).

without nest cavities on the study plots confirmed this prediction. Nest snags had significantly more bark cover than non-nest snags (69% vs. 54%,  $P = 0.009$ ,  $F$  test). Bark cover on snags with nests averaged 60% for all bird species (Table 10). Mean bark cover was 50% or more on the nest

snags of 11 of 16 bird species. There was an inconsistent relationship between these results and the designation of birds preferring hard or soft snags based on the cluster analysis (Fig. 7). Species using hard snags used snags with varying amounts of bark cover. Because a bark covering can indicate both soft snags (older snags with a bark covering retain warmth and moisture and are probably highly decayed) and also hard snags (trees dead only a short time; bark has not fallen and decay has not yet advanced), we recommend classifying tree hardness based on decay states.

*Size.*—Mean height of all nest trees (live and dead) was 12 m, ranging from 4 m for the white-headed woodpecker to 25 m for the brown creeper (Table 11). Mean diameter (dbh) of all nest trees was 62 cm, ranging from 44 cm for the hairy woodpecker to 84 cm for the red-breasted sapsucker. Mean height and diameter of trees available for nesting was 8 m and 32 cm, respectively. There were distinct differences in nest tree heights among the cavity-nesting birds, but nest tree diameters varied less. All species preferred large-diameter trees (Table 11). Thus, we conclude that tree diameter is a major character that identifies potential nest trees

Table 11. Comparisons of nest tree dimensions among cavity nesting birds.

Bird species	Mean dimension			
	Nest tree height (m)	Nest tree dbh (cm)	Nest hole height (m)	Tree diameter at hole (cm)
White-headed woodpecker	3.8 A <sup>a</sup>	64.6 ABCD	2.0 A	61.2 CD
Pygmy nuthatch	6.1 A	45.8 AB	4.7 AB	39.1 AB
Mountain bluebird	6.6 A	45.4 AB	4.5 AB	37.9 A
Mountain chickadee	8.1 A	56.0 AB	3.5 AB	49.1 BC
House wren	9.3 AB	51.8 AB	4.1 AB	47.6 ABC
White-breasted nuthatch	10.2 AB	63.9 ABC	5.7 AB	54.3 CD
Tree swallow	10.3 AB	50.8 AB	4.6 AB	40.2 ABC
American kestrel	10.4 AB	78.3 CD	8.1 BCD	59.7 CD
Lewis' woodpecker	11.4 B	66.5 BCD	7.3 BC	52.2 CD
Northern flicker	12.7 B	60.9 ABC	7.7 BC	43.8 ABC
Hairy woodpecker	13.7 B	43.8 A	4.8 AB	36.1 A
Red-breasted nuthatch	15.1 B	70.1 BCD	9.2 CD	44.0 ABC
Black-backed woodpecker	16.8 BC	44.5 AB	2.8 AB	39.7 ABC
Williamson's sapsucker	19.9 C	81.6 D	11.2 DE	54.2 CD
Red-breasted sapsucker	20.5 C	84.1 D	12.8 E	53.9 CD
Brown creeper	25.1 D	67.5 BCD	2.1 A	66.6 D
All species	12.3	62.3	6.5	48.4

<sup>a</sup> Within each column, means with the same letter are not significantly different ( $P > 0.05$ , Duncan's multiple range test).

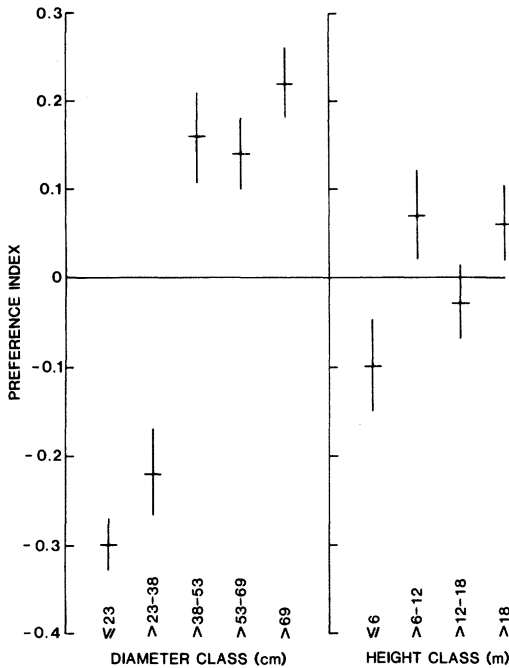


Fig. 8. Preference index values (use minus availability) for height and diameter classes of snags used for nesting by all species of cavity-nesting birds. Vertical lines indicate 95% confidence intervals of index values.

among available trees and that bird species then select among large-diameter trees mostly on the basis of tree height.

To continue the analysis of tree size preferences, we arbitrarily created 5 diameter and 4 height categories and computed frequencies of use and availability within each category. The availability frequencies were computed by weighting the total number of snags on each study plot such that the number of snags we included in each forest type was proportional to the number of nests occurring in that type. Larger diameter snags (>38 cm dbh) were preferred (Fig. 8). Preference did not increase with tree height, except that trees shorter than 6 m were used less than predicted from our estimate of their availability.

These results suggested again that diameter was the tree characteristic most closely correlated with nesting use. If so, preference for tall trees might be an artifact of the correlation between tree

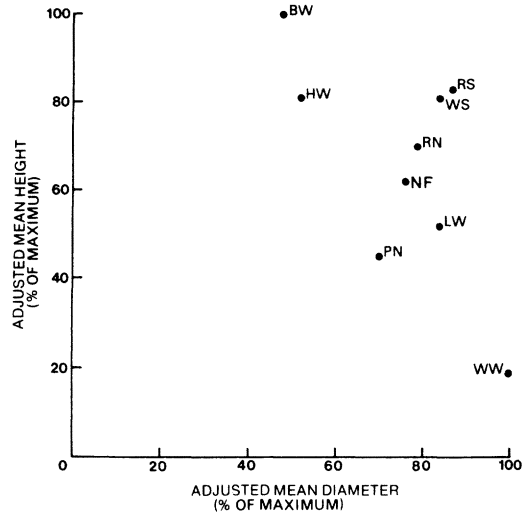


Fig. 9. Relative mean nest height (adjusted for tree diameter) and diameter (adjusted for tree height) of excavators. See text for adjustment methods. Bird name codes are given in Table 1.

height and diameter. Because this relationship varied with tree species, we performed 2 analyses of covariance comparing mean tree heights among the birds and among the tree species adjusting for diameter, and then we compared mean diameters adjusting for height (Fig. 9). For these analyses, we selected only nest sites of the 9 excavator species, the birds that initially chose nest trees. To increase the sample size in each cell, we used only the pooled categories of fir and pine in the analysis. We found significant interspecific differences in adjusted diameter ( $F = 6.1$ ,  $P = 0.001$ ) and height ( $F = 10.7$ ,  $P = 0.001$ ). Later (post-hoc) analyses testing differences of adjusted mean tree diameters among the bird species showed that white-headed woodpeckers (which selected the largest diameter trees) and black-backed woodpeckers and hairy woodpeckers (which selected the smallest trees) exhibited the strongest preferences for nest tree diameters. A similar analysis of adjusted mean heights showed that pygmy nuthatches, black-backed woodpeckers, and white-headed woodpeckers were the most selective for tree height (Fig. 9).

We found differences in nest hole height

Table 12. Statistics derived from discriminant analysis of nest tree characteristics among excavators ( $N = 299$ ).

Variable	Correlation with discriminant score			Entry level <sup>a</sup>
	I	II	III	
Tree condition (live or dead)	0.72	0.24	-0.07	3*
Tree diameter	-0.57	0.09	0.45	2*
Tree height	-0.83	0.04	-0.27	1*
Top (broken or intact)	-0.32	-0.47	-0.44	5*
Foliage-bearing twigs (present or absent)	-0.81	-0.12	-0.11	10
White fir	0.11	0.51	-0.07	8*
Jeffrey pine	0.42	0.17	0.25	7*
Lodgepole pine	-0.37	-0.25	-0.23	9
Red fir	-0.04	-0.69	0.10	4*
Bark cover <sup>b</sup>	-0.47	0.17	0.32	6*
Explained variance	0.40	0.13	0.08	
Cumulative explained variance	0.40	0.53	0.61	

<sup>a</sup> Step at which variables entered in stepwise analysis.<sup>b</sup> Arcsine transformed.\* Variables that add significantly ( $P < 0.01$ ) to discrimination between groups, given the variables already entered.

and tree diameter at hole height (DHH) among the cavity-nesting bird species (Table 11). Again, these analyses ignored possible confounding influences of interspecific differences in tree height and diameter preference. We reanalyzed the data, again selecting only the excavator species, using analysis of covariance. We found no differences among species in mean nest hole height when the effects of tree diameter, tree height, and tree top presence or absence were removed ( $F = 1.6$ ,  $P = 0.112$ ). The covariates explained 70% of the total variance in nest hole height, but differences among bird species explained only 1%. Most nests were located near the top of the tree, usually within 1 m if the top was broken. Interspecific variation in nest height seemed to reflect differences in the height of the trees selected for nesting rather than differences in hole location in trees of equal height.

Similarly, we used analysis of covariance to compare DHH among bird species adjusting for tree diameter (dbh) and tree height. Again, we found no differences among species ( $F = 1.1$ ,  $P = 0.356$ ). The covariates explained 62% of the interspecific variation in DHH, but differences among bird species explained only 1%. Neither of these analyses suggested that all excavators locate nests at the same

height or the same diameter. Rather, if all species chose trees of the same overall height, diameter, and top condition their nests would be the same height and the trees would be the same diameter at the height of the nest. Perhaps these birds have different preferences, and they select trees of sufficient size to meet their preferences for nest height and DHH.

*Discriminant Analysis of Nest Tree Characteristics.*—As with tree size, variables describing nest tree characteristics were correlated with each other. Thus, conclusions based on analyses of single variables only are weakened by possible confounding effects of other variables. Discriminant analysis allows the simultaneous evaluation of a set of variables while taking into account their intercorrelations. We used stepwise discriminant analysis to test for differences among nest trees (both live trees and snags) of all excavator species and to assess the relative association of each variable with observed differences. We limited the analysis to excavators because these species selected the trees.

Ten variables were used in the analysis (Table 12). Dichotomous variables were assigned a value of 0 if the feature was absent or 1 if present. Tree condition was coded with 0 if alive or 1 if dead. Three discriminant functions added at least 5%



Table 13. Comparisons of mean discriminant scores among excavators ( $N = 299$ ), based on nest tree characteristics.<sup>a</sup>

Species <sup>b</sup>	PN	RN	BW	HW	NF	LW	WW	WS	RS
PN		5.55*	2.12	2.32	4.57*	1.61	0.12	9.32*	9.37*
		1.22	4.70*	2.21	0.48	1.27	5.75*	2.34	0.26
		0.66	2.95	3.90*	0.34	0.93	3.45*	1.28	0.49
RN	1.50		1.40	2.63	1.97	4.29*	4.26*	3.21*	3.28*
			4.04*	1.24	0.86	2.49	4.97*	1.11	1.01
			3.39*	4.55*	0.45	0.24	2.99	0.56	1.25
BW	2.50	2.29		0.41	0.39	1.13	1.89	3.30*	3.34*
				3.01	4.74*	5.60*	0.12	3.56*	4.78*
				0.20	3.33*	3.59*	5.12*	3.84*	2.80
HW	1.50	1.58	1.35		1.30	1.01	1.93	5.61*	5.67*
					2.13	3.46*	3.66*	0.39	2.21
					4.77*	4.93*	6.29*	5.42*	3.86*
NF	1.03	0.48	2.30	1.39		3.05	3.29*	6.30*	6.37*
						2.08	5.97*	2.39	0.03
						0.77	3.54*	1.22	1.04
LW	0.56	1.22	2.78	1.72	0.77		1.30	8.28*	8.34*
							6.89*	4.02*	1.73
							2.90	0.32	1.61
WW	2.39	2.54	2.64	2.86	2.50	2.60		6.73*	6.78*
								4.49	5.94*
								2.78	4.02*
WS	2.29	0.79	2.50	2.11	1.28	2.00	2.85		0.10
									2.44
									2.09
RS	2.22	0.85	2.61	1.95	1.21	1.89	3.30	0.65	

<sup>a</sup> Numbers below the diagonal are the Euclidian distances among species as measured in 3-dimensional discriminant space. The sets of numbers above the diagonal are the 3  $t$  values indicating the significance of the difference between mean discriminant scores along each of 3 axes. The value associated with the first discriminant axis is listed first, followed by values for the second and third axes.

<sup>b</sup> See Table 1 for bird name codes.

\* Significant differences between mean discriminant scores (values >3.19, the critical value for 36 comparisons with 290 df at  $P < 0.05$ ).

each to the explained variance. The 3 functions together explained 61% of the total variance (Table 12).

The first discriminant function was dominated by nest tree height, presence or absence of foliage-bearing twigs, and tree condition (Table 12). The second function was most closely correlated with nest tree species (the 2 firs) and presence or absence of top. The third function was most closely correlated with nest tree diameter, top condition, and the amount of bark remaining on the stem.

To compare nest trees of bird species, we tested all pairwise differences between mean discriminant scores among all excavators using a planned analysis with a family error rate of 0.05% (Table 13). Because all discriminant functions are independent, a significant difference between species along any single axis indicated that

the birds were selecting statistically distinct nest trees. All but 5 of the 36 possible species pairs showed a significant difference on at least 1 axis (Table 13). Differences were not demonstrated between the pygmy nuthatch and Lewis' woodpecker, red-breasted nuthatch and northern flicker, black-backed woodpecker and hairy woodpecker, northern flicker and Lewis' woodpecker, or red-breasted and Williamson's sapsucker. Were these species pairs potential competitors? With 1 exception, we think not.

The red-breasted nuthatch and northern flicker nested in quite distinct habitats (forest type overlap value = 0.61, Raphael 1980); the nuthatch preferred unburned pine-fir forest, and the flicker preferred burned pine-fir forest (Table 3). The pygmy nuthatch, Lewis' woodpecker, and northern flicker nested in burns that gen-

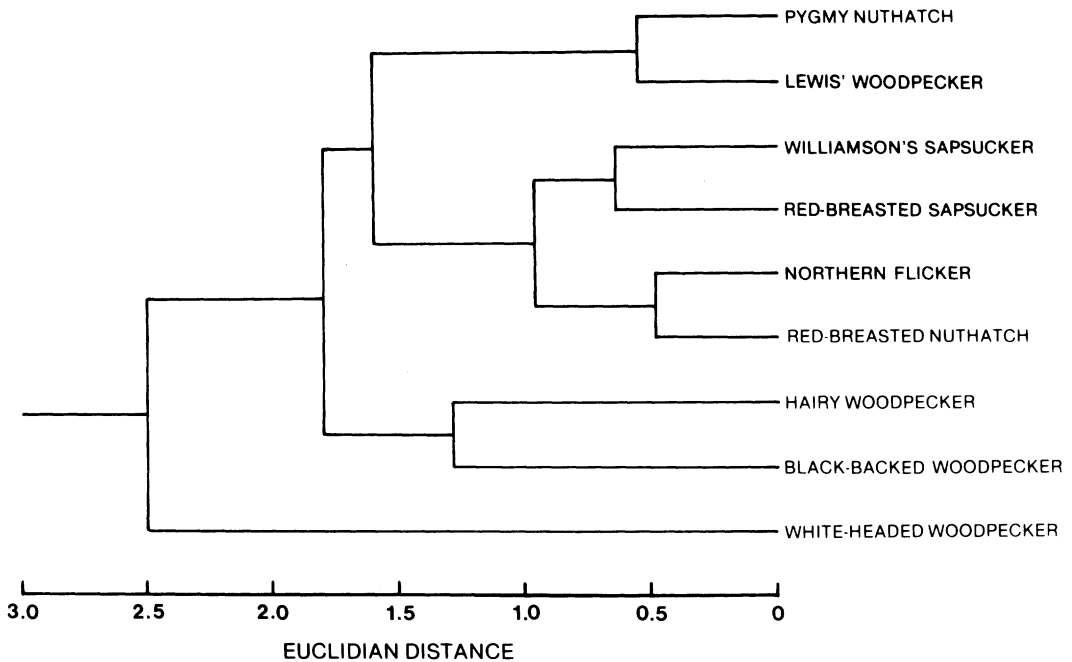


Fig. 10. Dendrogram showing similarity of nest trees of excavators based on Euclidian distances among mean discriminant scores (Table 13).

erally contained such a large number of snags that snag density probably did not limit their numbers. The black-backed woodpecker and hairy woodpecker overlapped only slightly in forest type (overlap value = 0.47, Raphael 1980), with more hairy woodpecker nests in pine-fir types and more black-backed nests in red fir types (Table 3). However, these species were represented by relatively few nests, which reduced the power of the statistical tests performed.

Williamson's and red-breasted sapsuckers, however, may compete more directly. These species showed high overlap in forest types used for nesting (overlap value = 0.97, Raphael 1980). Furthermore, they were ranked second only to the pygmy nuthatch-Lewis' woodpecker pair in overall similarity of nest sites measured by their Euclidian distance in discriminant space (Table 13). These 2 species are closely related phylogenetically (Short and Morony 1970) and forage in a similar fashion. Finally, Young (1975) presented

convincing evidence of interspecific territoriality between Williamson's and yellowed-bellied sapsuckers in New Mexico. Our observations of the spatial distribution of nests of these 2 sapsuckers at Sagehen Creek suggested that they located nests as if they were interspecifically territorial; no nests of 1 species were found closer to the other species than the average distance between its own nests.

The degree of nest site similarity between all excavators is shown graphically in a dendrogram (Fig. 10), which groups species according to a UPGMA cluster analysis of the Euclidian distance between the mean discriminant scores from Table 13. The 4 closely related pairs discussed above are shown. Not evident in the dendrogram is the close relationship of the northern flicker and Lewis' woodpecker nests. However, inspection of Table 13 shows that the rather distant linkage of the northern flicker and Lewis' woodpecker resulted from the close similarity of nest sites of the red-breasted nuthatch

and the 2 sapsuckers and the lack of similarity of the sapsuckers and Lewis' woodpecker nest sites. The white-headed woodpecker was not linked closely with any other species. The first discriminant function, which accounted for most of the interspecific variation in nest tree characteristics, was identified by tree size, twig presence, and tree condition. Only the white-headed woodpecker was located at the positive extremity of this axis. It nested in the oldest, softest snags, which were short and had large diameters, and no twigs.

*Discriminant Analysis of Nests in Snags.*—The preceding discriminant analyses considered nests in both live trees and snags. We performed 2 additional analyses including only snags. The first compared nest snag characteristics among the excavators, and the second compared nest and non-nest snags. For the interspecific analysis, we derived 3 discriminant axes, which together accounted for 62% of the total variation in nest snags (Table 14). The first axis was identified by tree size (height and diameter) and relative decay (twig and bark presence). The second axis was correlated with condition of top, tree height, and tree species, and the third axis was correlated with red fir and tree size. The variable that best discriminated among species' nest sites was tree

Table 14. Correlation of nest snag variables with discriminant scores derived from analysis of excavator nests in snags ( $N = 214$ ).

Variable	Discriminant function <sup>a</sup>		
	I	II	III
Diameter	0.67	−0.08	0.34
Height	0.64	−0.58	−0.32
Top	0.03	−0.74	−0.35
Foliage-bearing twigs	0.42	−0.32	−0.01
White fir	0.18	0.32	−0.30
Jeffrey pine	−0.16	0.48	−0.08
Lodgepole pine	0.17	−0.53	−0.07
Red fir	−0.30	−0.53	0.60
Bark cover (%)	0.49	0.25	0.14
Explained variance	0.38	0.18	0.10
Cumulative explained variance	0.38	0.52	0.62

<sup>a</sup> Correlations >0.13 or <−0.13 are significant at  $P \leq 0.05$ .

height; it had the highest univariate  $F$  ratio and was, thus, the first variable to enter into the discriminant function equation (Table 15). All variables except foliage-bearing twigs and white fir contributed significantly to this discrimination among bird species.

The second analysis was based on the 952 snags on 7 bird census plots. Of these, 62 contained excavated nest cavities and were considered nest snags for comparison with the remaining 890 non-nest snags. Nest snags differed significantly from non-nest snags in mean diameter, top condi-

Table 15. Discriminant analyses comparing characteristics of (1) nests in snags among excavator species and (2) snags with nest holes vs. snags without holes on the study plots.

Variable	Means			Rank of univariate $F$ ratio		Step entered	
	Among spp. $N = 214$	Nest $N = 62$	Non-nest $N = 890$	Among spp.	Nest vs. non-nest	Among spp.	Nest vs. non-nest
Diameter (dbh, cm)	62.1	49.4	29.3	3*	1*	6**	1**
Height (m)	11.5	8.2	8.3	1*	9	1**	5
Top	0.21	0.11	0.41	2*	2*	3**	3**
Foliage-bearing twigs	0.16	0.15	0.18	6*	7	9	4
White fir	0.50	0.51	0.33	9	4*	8	8
Jeffrey pine	0.21	0.20	0.22	7*	8	7**	9
Lodgepole pine	0.14	0.16	0.26	8*	5	5**	7
Red fir	0.13	0.10	0.18	4*	6	2**	6
Bark cover (%)	0.72	0.75	0.42	5*	3*	4**	2**

\* Significant  $F$  ratios ( $P < 0.05$ ).  
\*\* Variables that contribute significantly ( $P < 0.01$ ) to the discrimination among groups, given variables already entered in equation.

tion, bark cover, and proportion that were white fir (Table 15). In marked contrast to the previous analysis comparing snag characteristics among bird species (Table 15), mean height did not differ between nest and non-nest snags. Diameter, bark cover, and top condition were the only variables that contributed significantly to this discrimination between nest and non-nest snags (Table 15). Nest snags were larger in diameter, had more bark, and more often had a broken top. The discriminant function equations segregated the total sample into nest and non-nest categories with 84% accuracy. Among non-nest snags, 16% were misclassified as nest snags. Perhaps these were suitable nest sites in which birds had not yet dug cavities.

*Relative Importance of Stand and Nest Tree Variables.*—Did the observed differences in nest stand structure among bird species (Table 5) influence the analysis of interspecific nest tree differences (Table 12)? We performed 2 additional multi-group stepwise discriminant analyses to examine such effects using tree and habitat variables combined (see Tables 5 and 12 for variables lists). First, we entered the tree variables as a group, followed by the habitat variables. The tree variables explained 67% of the total variation. With the effect of these tree variables removed, all stand variables except number of snags >38 cm still contributed significantly to the discrimination between bird species, and together the stand variables explained an additional 16% of the variation. For the next analysis, we entered the stand variables first, followed by the tree variables. When entered first, the stand variables explained 61% of the variation. With the effect of the stand variables removed, the tree variables explained an additional 22% variation, and all variables except lodgepole pine and foliage-bearing twigs contributed significantly. Thus, tree variables were slightly better discriminators, but both tree and stand variables contributed to the interspecific differences in nest sites.

## Nest Cavity Characteristics

*Cavity Source.*—Nonexcavators depend on excavators or existing cavities for nest sites. For each active nest, we assigned the probable source of the cavity based upon our observations and measurements of the size and shape of cavities excavated by each species. Hairy woodpeckers and northern flickers apparently dug most of the excavated cavities occupied by nonexcavators (Table 16). Existing cavities were occupied primarily by mountain chickadees (43% of their nests) and brown creepers (100%). Only 12 nests of 5 other bird species were found in existing cavities. Excavators were the most important source of cavities occupied by all nonexcavator species except for brown creepers and mountain chickadees. The mountain chickadee excavated 13% of the cavities it used for nesting (usually in well-rotted white fir snags) and used excavator cavities for 44% of its nests. White-breasted nuthatches excavated 15% of their own nests whereas 20% were in existing cavities. The remaining 65% were in excavator cavities (Table 16). Mountain chickadees and white-breasted nuthatches are facultative excavators. Factors leading to their choice of hole excavation vs. occupation of cavities are unknown. Perhaps when suitable cavities are scarce, these birds dig their own.

*Cavity Size.*—Not surprisingly, size of the entrance hole and cavity varied with size of the cavity-nesting species. We measured 6 variables describing 335 nest cavities of 16 species (Table 17). The smallest cavity entrances (approximately 30 mm) were excavated by the smallest birds (pygmy and red-breasted nuthatches) and the largest (approximately 60 mm) by the largest birds (northern flicker and Lewis' woodpecker). The intermediate-sized birds excavated moderate-sized cavity entrances (approximately 35–50 mm). Cavity entrance diameter also was highly correlated with internal cavity size ( $r = 0.73$  with cavity depth and with internal diameter).

Table 16. Probable source of cavities used by cavity occupants at Sagehen Creek.

Cavity occupant <sup>a</sup>	Cavity source													Existing cavity <sup>b</sup>	Total
	PN	RN	HW	BW	WW	WS	RS	NF	LW	MC	WN	Unknown excavator			
PN	24		1											2	27
RN		27					2								29
HW			23												23
BW				7											7
WW					12										12
WS						41									41
RS							48								48
NF					1 <sup>c</sup>	1 <sup>c</sup>	1 <sup>c</sup>	63							66
LW									34						34
MC	2	5	11	3	3	8	8	3		15		8	50		116
WN	1		2			1	2	3			3	4	4		20
AK								9	4						13
MB			10	1	1		1	21	1			1	1		37
WB			1					1							2
TS			9				1	1						1	12
HR	1		6	3		1		3				3	4		21
ES			1				1								2
BC														16	16
Total <sup>d</sup>	4	5	41	7	5	11	16	41	5			16	78		526

<sup>a</sup> See Table 1 for bird name codes.  
<sup>b</sup> Any cavity not created by excavator, e.g., space behind bark, cavities resulting from decay or cracks, etc.  
<sup>c</sup> Cavity subsequently enlarged by NF.  
<sup>d</sup> Totals (except grand total) excluding cavities excavated by occupant.

Table 17. Dimensions of cavities occupied by nesting birds.

Bird <sup>a</sup>	Cavity dimension												Sample size
	Hole height (m)		Tree diameter at hole (cm)		Minimum diameter of entrance (mm)		Cavity depth (cm)		Internal diameter of cavity (cm)		Sill width (cm)		
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	
AK	3.8	0.48	41.8	6.61	66.5	3.93	32.0	5.05	20.0	3.16	2.3	0.75	4
MC	2.4	0.21	46.3	2.65	34.8	1.15	17.7	1.20	11.2	0.41	3.8	0.36	94
BC	1.6	0.27	56.9	4.34	28.1	2.79	5.4	2.06	7.8	1.09	0.5	0.34	10
MB	3.9	0.26	38.3	2.78	51.0	1.72	19.3	1.23	13.7	0.60	3.7	0.29	29
HR	2.9	0.86	41.3	4.59	44.4	3.64	14.0	2.67	9.2	0.64	3.8	0.72	9
PN	4.5	0.31	34.9	1.93	29.8	1.32	15.6	0.56	8.3	0.55	2.8	0.32	23
RN	5.4	0.92	40.0	5.37	30.5	1.60	14.6	1.24	8.2	0.71	3.4	0.47	11
TS	3.3	0.52	37.8	2.55	42.4	3.18	20.3	1.49	11.5	0.39	3.8	0.30	11
WN	3.1	0.51	58.0	8.68	40.3	2.99	19.6	1.64	15.9	1.41	4.5	0.79	16
BW	2.8	0.59	38.3	3.12	44.3	1.53	20.6	1.46	11.1	0.69	4.4	0.71	8
HW	4.9	0.69	36.3	2.09	44.8	1.40	21.4	1.01	12.4	0.48	4.7	0.34	16
NF	4.0	0.28	40.1	1.56	62.8	0.97	33.9	1.40	16.1	0.50	4.2	0.37	40
LW	5.0	0.25	52.0	3.83	62.1	1.58	33.7	1.39	16.5	0.56	3.3	0.31	23
WW	1.9	0.26	58.8	9.82	45.7	2.72	21.3	0.86	12.8	0.48	4.1	0.43	12
WS	4.4	0.50	50.9	3.37	41.6	0.67	20.1	1.01	13.5	0.55	4.9	0.31	17
RS	4.1	0.62	46.3	5.69	37.7	1.33	17.9	0.97	10.7	0.75	4.7	0.40	13

<sup>a</sup> See Table 1 for bird name codes.

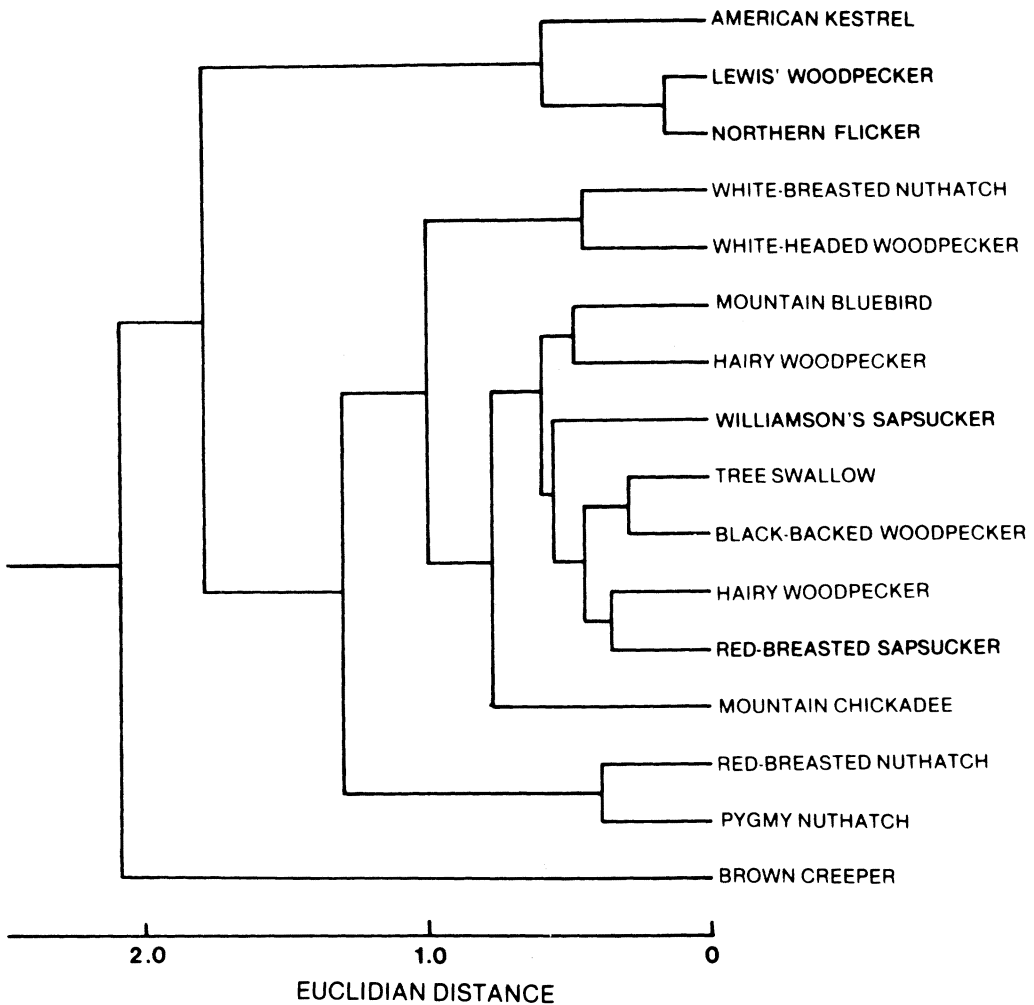


Fig. 11. Dendrogram showing groups of bird species that use cavities of similar dimensions, based on Euclidian distances among mean factor scores.

We used a principal components analysis to transform the original set of 6 intercorrelated cavity size variables (Table 17) to a new, reduced set of independent variables. In this case, 3 new variables (factors) were produced that explained 72% of the total variance in cavity size. The first factor, explaining 33% of the variance, was most strongly correlated with cavity size (entrance diameter, cavity diameter, and cavity depth). The second factor, explaining 21% of the variance, was correlated with hole height and

tree diameter at the hole, and the third factor, explaining 18%, was correlated with sill width. We then computed the mean score on each of the 3 factors for each bird species and computed the Euclidian distance between each bird in this 3-dimensional space (Raphael 1980). From this matrix of distances we used a UPGMA cluster analysis to construct a dendrogram showing groups of species that used cavities of similar dimensions (Fig. 11). The maximum distance (greatest dissimilarity) between species was 2.2 units. At half of

Table 18. Similarity<sup>a</sup> of excavator and nonexcavator nest sites.

Excavators	Nonexcavators						
	AK <sup>b</sup>	MC	BC	MB	HR	TS	WN
PN	1.56*	1.58 <sup>c</sup>	3.44	0.46*	1.01* <sup>c</sup>	2.02	1.44 <sup>c</sup>
RN	2.78	2.00 <sup>c</sup>	2.39	2.91	2.85	3.17	1.42
BW	2.80	1.66 <sup>c</sup>	2.41	2.00 <sup>c</sup>	1.35* <sup>c</sup>	1.97	1.96
HW	2.39	1.69 <sup>c</sup>	2.70	1.34* <sup>c</sup>	1.01* <sup>c</sup>	1.77* <sup>c</sup>	1.77 <sup>c</sup>
NF	1.28* <sup>c</sup>	1.31	2.65	1.12	1.07*	1.94	0.94*
LW	1.16* <sup>c</sup>	2.29	3.07	1.56 <sup>c</sup>	1.27*	2.02	1.83
WW	2.11	1.92 <sup>c</sup>	2.14	2.60	2.50 <sup>c</sup>	2.98	1.54 <sup>c</sup>
RS	2.42	2.26 <sup>c</sup>	2.05	2.75 <sup>c</sup>	2.65	2.94 <sup>c</sup>	1.73 <sup>c</sup>
Nest mean <sup>d</sup>	1.22	1.56		1.63	1.39	2.22	1.48
Non-nest mean <sup>e</sup>	2.24	2.29	2.71	1.99	1.98	2.36	1.66

<sup>a</sup> Euclidian distance between discriminant score (computed from nest tree and nest stand variables) of each excavator and nonexcavator.  
<sup>b</sup> See Table 1 for bird name codes.  
<sup>c</sup> Indicates known excavators of cavities occupied by that particular nonexcavator. For example, AK cavities are excavated by NF and LW. See Table 16 for data on cavity source.  
<sup>d</sup> Mean distance among species identified as excavators of cavities occupied by each nonexcavator.  
<sup>e</sup> Mean distance to other excavators.  
\* Distances not significantly >0.0 (multivariate *F* test, *P* > 0.05).

this distance (1.1 units) there were 4 groups of species: those excavating or using large cavities (American kestrel, Lewis' woodpecker, northern flicker), 9 species using medium-sized cavities (white-breasted nuthatch through mountain chickadee), 2 small-cavity species (red-breasted and pygmy nuthatches), and the isolated brown creeper. Comparison with Table 16 shows that nonexcavators usually were clustered with the excavators whose cavities they used, although mountain bluebirds were clustered with hairy woodpeckers even though most bluebird nests were excavated by northern flickers. Pair-wise contrasts testing for differences between mean factor scores within each group showed no significant differences. Tests of pairs across groups were significant. The brown creeper was not linked closely with any other species because of its unique habit of nesting in the space between loose bark and wood. It had the shallowest cavity and narrowest sill width (Table 17).

*Comparison of Nests of Excavators and Nonexcavators.*—Birds differ in the cavities they excavate or use, in the trees they select for nesting, and in the stand characteristics around the potential nest. Thomas et al. (1976), Bull (1978), Conner (1978), and others have suggested that

habitat management that meets the requirements of the excavators also will meet those of the nonexcavators. To test the validity of this hypothesis, we compared nest tree and nest stand characteristics of each excavator with those of each nonexcavator, using the Euclidian distances among their centroids in discriminant space (Table 18). Smaller values indicate more similar nest sites. For each nonexcavator there was at least 1 excavator species whose nest characteristics were statistically matched, except for the brown creeper, which was statistically distinct from every excavator.

In Table 18, excavators known to create cavities used by a nonexcavator are indicated. For each nonexcavator, we computed the mean Euclidian distance to those source excavators and compared it to the mean distance among the remaining excavators (those whose cavities were not used by that nonexcavator). In each case, as one would expect, the mean distance to the species whose cavities were used was less than the distance to those species whose cavities were not used. Apparently, excavator management can meet nonexcavator requirements for nest trees and nest stands for these species, except for the brown creeper. Brown creeper nest site requirements are not met by managing for excavators; creeper habitat needs

should be recognized explicitly in snag management plans.

### Foraging Site Characteristics

*Foraging Substrate.*—We studied foraging behavior of 10 of the cavity-nesting bird species. We recorded 1,026 observations of substrate use. Elimination of repeated observations of a particular bird on the same tree left 663 observations for analysis. Of this total, 30% occurred on snags, 61% on live trees, and 9% on logs, ground, brush, or in the air (Table 19).

A crude estimate of the expected proportion of snag use can be obtained by comparing the numbers of live and dead stems counted on our 100 random plots. Only 9% of the stems on the random plots were dead, compared to 33% among the foraging observations, indicating that birds were selecting snags as feeding sites (binomial test,  $P < 0.05$ ). Hairy and Lewis' woodpeckers used snags most frequently. With these species excluded from analysis, 17% of the trees used for foraging by the remaining birds were dead, still significantly higher than expected ( $P < 0.05$ ).

These results suggest an overall preference for snags by the birds. We assumed that availability of dead trees on the random plots reflected the actual availability in the home ranges of the birds under study. The plots were located randomly over the whole basin, but the birds nested selectively among the forest types. Snag densities varied among these types. We plotted differences between the relative numbers of observed and expected foraging bouts in each of 6 broad forest types (Fig. 12). The expected proportions were based on the frequency of occurrence of forest types among the random plots. The proportions were similar, except that significantly more birds were observed foraging in unburned pine-fir forest (binomial test,  $P < 0.05$ ).

A second assumption was that birds were equally observable on each substrate. We followed birds from substrate to substrate and recorded each new choice made by the bird. By following individual

birds we reduced the bias involved in differential observability on first sighting. The preceding analysis, involving simple totals, disregarded temporal sequence of substrate use. To incorporate this information, we calculated matrices of transition probabilities for each bird species (except Lewis' woodpecker) using methods suggested by Vandermeer (1972) and Colwell (1973). For this analysis, we combined logs, ground, and air into a nontree category. These matrices gave the probability of a bird moving from 1 site on a substrate to another site of the same, or to a different substrate. Incorporating information on average number of sequential observations of a bird on the same substrate (Colwell 1973), we computed a grain matrix ( $G$ ) of substrate to substrate transition probabilities for each bird (Table 20). The proportional visit rate of each bird (preference vector  $U$ ) at steady state was calculated by solving the equation  $UG = U$ . The elements of vector  $U$  are the values of the eigenvector associated with the matrix  $G$ . They can be interpreted as proportional long-term probability that a bird will be observed foraging on each of the 3 substrates. The probabilities associated with foraging on snags varied from lows of 0.0 and 0.04 for the pygmy nuthatch and brown creeper, respectively, to highs of 0.20 and 0.42 for the black-backed and hairy woodpeckers (Table 20).

The probabilities for snag and live tree use generated by this analysis were dependent on the value for nontree use, because all probabilities sum to 1.0. The ratio of live and dead tree probabilities was independent of the magnitude of the nontree use and was useful for interspecific comparisons (Table 20). The ratio of live to dead stems  $>15$  cm dbh found on the random plots was 10.5, a value exceeded by pygmy nuthatches, brown creepers, and red-breasted nuthatches. All other ratios were  $<10.5$ , indicating that the probability of those species foraging on snags was higher than expected based on the estimated availabilities of live and dead trees. These results reinforced the sugges-



Table 19. Percentage use and diversity of foraging sites and foraging methods of cavity-nesting birds.

Category	BW <sup>a</sup>	HW	RS	WW	WS	LW <sup>b</sup>	PN	RN	WN	BC	All observations
<b>Substrate</b>											
Live tree	61	47	73	71	85	14	67	88	67	85	61.1
Snag	21	51	21	28	14	66	9	6	16	11	29.9
Log	18	2	3	2	0	2	0	1	11	4	3.8
Ground	0	0	1	0	0	15	24	4	6	0	4.5
Brush	0	0	0	0	0	3	0	0	0	0	0.4
Air	0	0	1	0	1	0	0	0	0	0	0.3
Sample Size	33	139	71	51	71	88	33	69	81	27	663
Diversity <sup>c</sup>	0.94	0.78	0.75	0.68	0.46	1.02	0.83	0.46	0.97	0.51	
<b>Tree species</b>											
Jeffrey pine	15	28	14	49	39		72	39	72	41	38.8
Lodgepole pine	0	20	54	8	16		0	23	1	0	17.3
Red fir	49	12	9	20	27		4	12	7	4	14.9
White fir	6	40	22	24	16		24	23	18	52	25.9
Other	30	0	1	0	3		0	3	1	4	3.1
Sample size	30	139	69	51	70		25	66	76	27	566
Diversity	1.16	1.30	1.20	1.22	1.41		0.71	1.40	0.82	0.96	
<b>Position on tree</b>											
Trunk	100	79	78	53	77	68	28	32	61	94	64.0
Live branch	0	16	18	16	18	16	14	25	24	7	17.6
Dead branch	0	3	2	6	5	4	33	21	13	0	8.6
Foliage	0	2	2	26	0	12	25	22	2	0	9.8
Sample size	37	206	91	110	95	75	57	149	131	31	987
Diversity	0.00	0.66	0.66	0.15	0.66	0.94	1.34	1.37	0.99	0.24	
<b>Method</b>											
Gleaning	32	77	81	85	82	22	94	97	92	100	78.7
Drilling	68	23	9	12	8	2	5	3	7	0	12.1
Flycatching	0	0	10	0	1	76	2	0	1	0	7.9
Sapsucking	0	0	1	4	8	0	0	0	0	0	1.8
Sample size	37	186	93	110	96	88	65	152	136	31	994
Diversity	0.63	0.54	0.66	0.52	0.61	0.62	0.29	0.13	0.31	0.00	

<sup>a</sup> See Table 1 for bird name codes.<sup>b</sup> Tree species not recorded for LW.<sup>c</sup> Shannon-Wiener index ( $H'$ ).

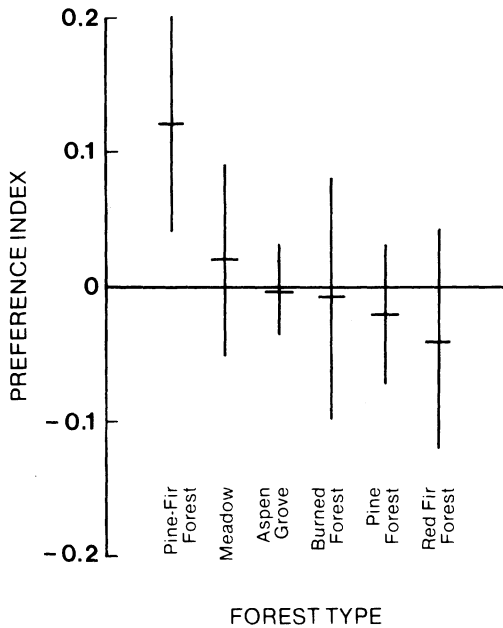


Fig. 12. Preference index values (use minus availability) for forest types used by foraging birds (all species). Vertical lines indicate 95% confidence intervals of index values.

tion that these birds selected snags for foraging, although the true snag availability within the home range of each bird was not measured.

Following the methods of Colwell (1973: 752), we calculated a grain matrix for all birds combined. To do so, we first calculated a transition matrix for each bird species. To combine these matrices for all birds, one must find the probability that the next bird will be species  $B_i$  given substrate  $S_i$ , that is,  $P(B_i|S_i)$ . Using Bayes' theorem, we know that

$$P(B_i|S_i) = [P(S_i|B_i) P(B_i)] P(S_i)^{-1}.$$

We used the data in Table 19 to calculate  $P(S_i|B_i)$ , which is the percent of observations in live trees, dead trees, and nontrees for each bird.  $P(B_i)$  is the proportional abundance of each bird, for which we used the relative number of nests we located for each species.  $P(S_i)$  is the relative abundance of each substrate type, which we estimated from the random plot sample. The combined matrix of transition probabilities was then used to compute the

combined grain matrix (Table 20) by incorporating the vector describing the average number of sequential observations of all birds on each substrate. On average, birds would be observed foraging on live trees on 82% of the occasions and on dead trees 14%, if they fed on live and dead trees in proportion to their occurrence on the random plots and spent equal time foraging on live or dead trees. We measured the length of time spent at each foraging site for each observation. Using a 2-way ANOVA, we compared mean foraging times on live and dead trees for each bird species and found no differences in mean time between substrates ( $F = 1.95$ ,  $P = 0.125$ ). The ratio of live to dead tree probabilities was 5.7, a value much lower than the expected value of 10.5, indicating much more than expected use of snags for foraging by these birds as a group (Table 20).

The advantage of the preceding analysis over a sum of observations in live trees vs. snags is that it reduces observer bias. Birds are easier to see on snags, and the first observation of a foraging bird may more likely be on a more visible substrate. By following individual birds from substrate to substrate and recording the transitions, this initial bias disappears.

To what extent is the substrate use of each bird flexible in relation to substrate availability? We have mentioned that snag availability was not measured within the home ranges of each foraging bird observed, but we did note the forest type in which a bird was observed. Snags comprised 39%, 14%, and 4% of the total stems in burns, meadow areas, and other forested areas, respectively (Raphael 1980). We tabulated the number of observations of each bird species in snags and in live trees in each of these 3 habitat types. If a bird is perfectly opportunistic (fine-grained), it will use snags in proportion to availability; as the proportion of snags available increases, snag use will increase. Conversely, birds that are specialists on a particular substrate type (coarse-grained) will use that type in excess of its relative availability.

Table 20. Grain matrices<sup>a</sup> and preference vectors for substrates used for foraging by bird species.

Bird <sup>b</sup>		Grain matrices (G)			Preference vectors (U)			Ratio live to dead trees (L:D)
		Live tree (L)	Dead tree (D)	Nontree (NT)	L	D	NT	
BW	L	0.950	0.050	0				
	D	0	0.800	0.200	0.735	0.203	0.061	3.6
	NT	0.606	0.061	0.333				
HW	L	0.894	0.106	0				
	D	0.145	0.855	0	0.78	0.422	0	1.4
	NT	0	0	0				
RS	L	0.909	0.061	0.030				
	D	0.373	0.627	0	0.838	0.137	0.025	6.1
	NT	1.000	0	0				
WW	L	0.939	0.061	0				
	D	0.300	0.700	0	0.831	0.169	0	4.9
	NT	0	0	0				
WS	L	0.940	0.060	0				
	D	0.417	0.583	0	0.874	0.126	0	6.9
	NT	1.000	0	0				
PN	L	0.775	0	0.225				
	D	0.299	0.701	0	0.816	0	0.184	
	NT	1.000	0	0				
RN	L	0.933	0.027	0.040				
	D	0.558	0.442	0	0.889	0.075	0.036	11.9
	NT	0.500	0.500	0				
WN	L	0.889	0.069	0.042				
	D	0.464	0.432	0.104	0.816	0.133	0.051	6.1
	NT	0.561	0.374	0.065				
BC	L	0.957	0.043	0				
	D	1.000	0	0	0.959	0.041	0	23.4
	NT	0	0	0				
All species combined	L	0.909	0.043	0.048				
	D	0.284	0.710	0.007	0.815	0.142	0.043	5.7
	NT	0.795	0.148	0.058				
Expected ratio <sup>c</sup>								10.5

<sup>a</sup> Elements are transition probabilities from row to column. For example, for BW, the probability of moving from a live tree (L) to a dead tree (D) is 0.05.

<sup>b</sup> See Table 1 for bird name codes.

<sup>c</sup> Based on counts of live and dead stems on random plots.

A quantitative index of the degree of opportunism can be computed by calculating the correlation between relative snag density and snag use. We used a nonparametric test for trend in ordered contingency tables, Kendall's Tau, for this purpose (Marascuilo and McSweeney 1977: 446). If a bird is a perfect opportunist, Tau will equal 1.00; if its substrate selection is independent of availability, the value will equal 0. We plotted the relationship between snag use and availability for each species (Fig. 13) and for all birds

combined. Black-backed woodpeckers, hairy woodpeckers, and white-breasted nuthatches apparently were opportunistic. For these species, the proportion of snags used for foraging rose with increasing snag density. Tau was not significantly different from zero for any other species. The red-breasted sapsucker showed a high rate of snag use in habitats with high snag availability, but there were only 5 observations in the high availability class. This small sample does not justify labeling the sapsucker as opportunistic, especially con-

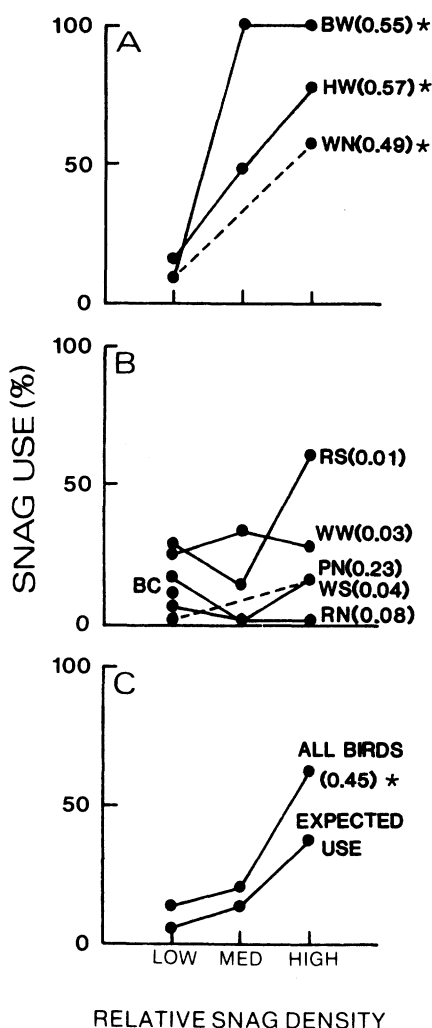


Fig. 13. Snag use (% of observations) by foraging birds in habitats with low, medium, and high snag density: (A) opportunistic species, (B) selective species, (C) all bird species, and expected percent use given random selection of live vs. dead trees in each snag density class. Values in parentheses (Kendall's Tau) measure the correlation between snag use and availability. Correlations significantly different from 0.0 are indicated with asterisks. White-breasted nuthatches and pygmy nuthatches (WN and PN), indicated with dashed lines, were not observed foraging in habitats with medium snag density; brown creepers (BC) were observed only in low snag density areas. See Table 1 for bird name codes.

sidering its low snag use when foraging in habitats with medium snag availability (Fig. 13).

Comparison of use of snags by each species of bird to expected use in each

class (Fig. 13) shows that all species except pygmy nuthatch, red-breasted nuthatch, and the Williamson's sapsucker foraged on snags in greater proportion than average snag availability in each class. This reinforced the results of the vector analysis of preference (Table 20) for all species except Williamson's sapsucker. Thus, snags are an important component in the foraging ecology of most of the birds we studied. Assuming that the frequency with which a foraging bird chooses a particular substrate reflects the energetic value of the prey obtained from it, snags may supply some particularly high energy prey (e.g., beetle larvae with low ratios of exoskeleton to soft tissue). Unfortunately, we can only speculate; no data were collected on food types supplied by each substrate or on the comparative rate at which prey were captured on each substrate. Experimental studies are needed to examine the response of birds to controlled densities of selected foraging substrates.

**Tree Size.**—Birds differed very little in the size of trees they selected for foraging. Trees used for foraging (excluding those used by Lewis' woodpecker) averaged 37 cm dbh and 16 m in height (Fig. 14). Trees used by Lewis' woodpecker were not included because these trees served only as perches between extended flycatching bouts. Diameters of live trees and snags did not differ (2-way ANOVA,  $F = 2.06$ ,  $P = 0.152$ ), but snags were significantly shorter (averaging 3 m less) than live trees, probably because most snags had broken tops. Planned pairwise contrasts of mean diameters of all trees among bird species showed significant differences between only the red-breasted nuthatch and red-breasted sapsucker. Similar contrasts of mean height showed that Williamson's sapsuckers and red-breasted sapsuckers were different than red-breasted nuthatches and white-breasted nuthatches; no other species pairs were significantly different.

To assess tree use by diameter class, we compared the frequency of occurrence of trees in each of 8 size classes on the random plots to the percent use in each class

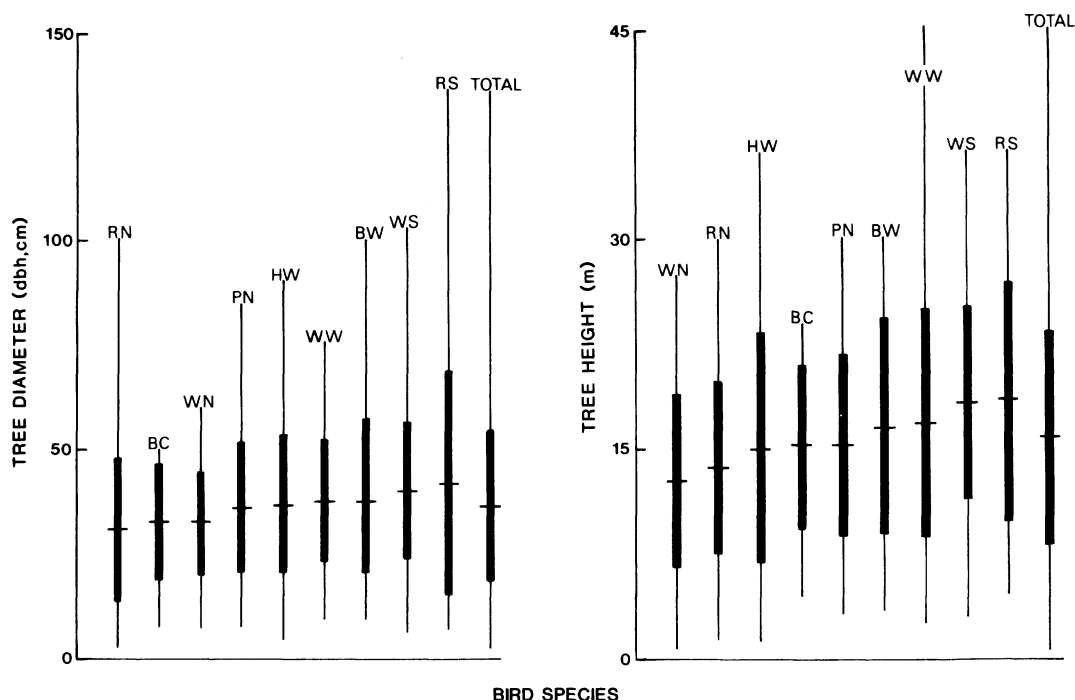


Fig. 14. Mean, standard deviation, and range of diameter and height of trees used for foraging by each bird species. See Table 1 for bird name codes.

using Strauss' (1979) index. The smallest trees ( $\leq 23$  cm dbh) were used proportionately less than their availability, medium trees ( $> 23$ – $53$  cm dbh) were used more than expected, and largest trees were used in the same proportion as their availability (Fig. 15).

Perhaps this pattern occurred because of the energetic cost of flying from tree to tree compared to the potential energetic benefit to be derived from each tree. Small trees were the most numerous and were closest together. Flight time between closer trees was lower and less energy was expended flying from tree to tree. But small trees have less available foraging surface area, and the number of available prey per tree is lower than in a large tree. A bird can feed longer on a large tree, and presumably can capture more prey per visit than on a small tree. Parker and Stevens (1979) found that larger diameter trees produced more beetle larvae per unit surface area than smaller trees, and Jack-

son (1979) showed that furrowed bark of larger trees supported larger numbers of insects than did the smoother bark of smaller trees. Our data also suggested that larger trees provide more food. Total foraging time per visit in the first 4 tree size classes (the only sizes with sufficient data for analysis) averaged 30, 36, 63, and 73 seconds, respectively. Medium-sized trees ( $> 38$ – $53$  cm dbh) received both the highest average foraging time per visit and the highest preference rating. Trees  $> 53$  cm dbh were used in proportion to availability, perhaps because their scarcity did not permit foraging specialization. To specialize on these largest, uncommon trees, a bird would have to fly long distances. If the trees had been evenly spaced, the average distance between trees  $> 53$  cm dbh would have been 70 m, whereas the distance separating those  $\leq 53$  cm dbh would have been only 6 m.

*Tree Species.*—Cavity-nesting birds fed primarily on Jeffrey pine (39%) and white

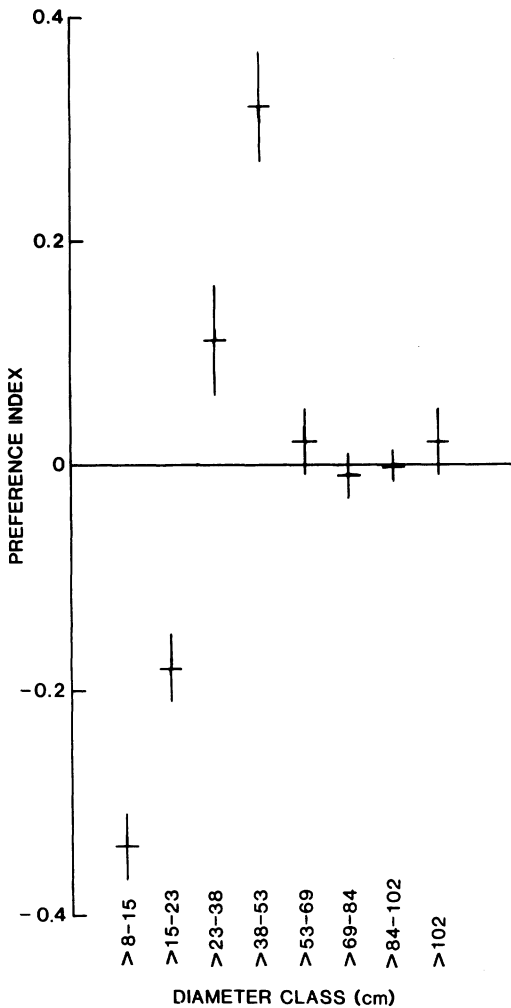


Fig. 15. Preference index values (use minus availability) for tree diameter classes used for foraging by birds (observations of all species grouped). Vertical lines indicate 95% confidence interval around each value.

fir (26%) trees. In relation to availability of tree species, as sampled on the random plots, birds foraged on Jeffrey pine more than expected and on lodgepole pine and white fir less than would be expected if they had selected substrates at random (Fig. 16). Red fir and trees in the "other" category were used in about the same proportion as their availability.

The Williamson's sapsucker, red-breasted nuthatch, and hairy woodpecker foraged on the widest variety of tree

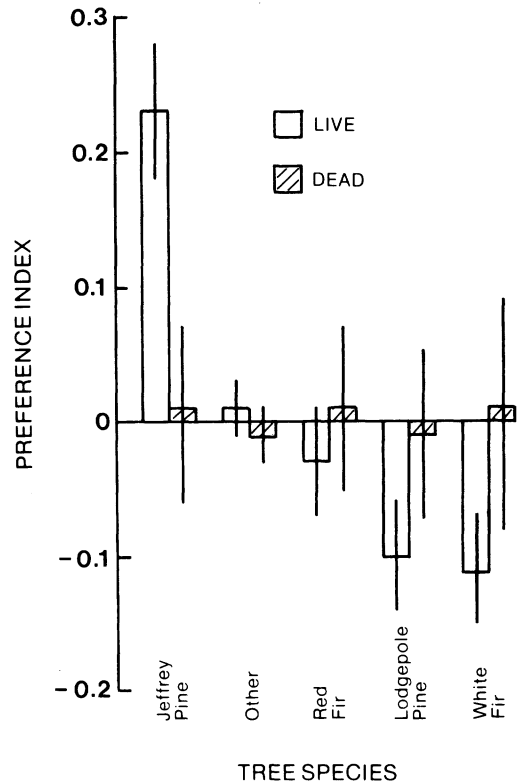


Fig. 16. Preference index values (use minus availability) for tree species used by foraging birds (all observations grouped). Vertical lines within bars indicate 95% confidence intervals.

species (Table 19). Pygmy nuthatches and white-breasted nuthatches were the most specialized. We used these frequencies of foraging observation to compute overlap values (Colwell and Futuyma 1971) between all pairs of bird species, excluding Lewis' woodpecker. These overlap values were then used in a cluster analysis, which revealed 2 groups of species (at overlaps  $>0.75$ ) separated primarily on the basis of heavy and light use of Jeffrey pine (Fig. 17).

We also calculated the number of foraging observations in snags of each tree species (Fig. 16). This group of birds foraged randomly with regard to snag species (percent use roughly equaled percent availability). Sample sizes were too small for an analysis of snag species use by each bird species.

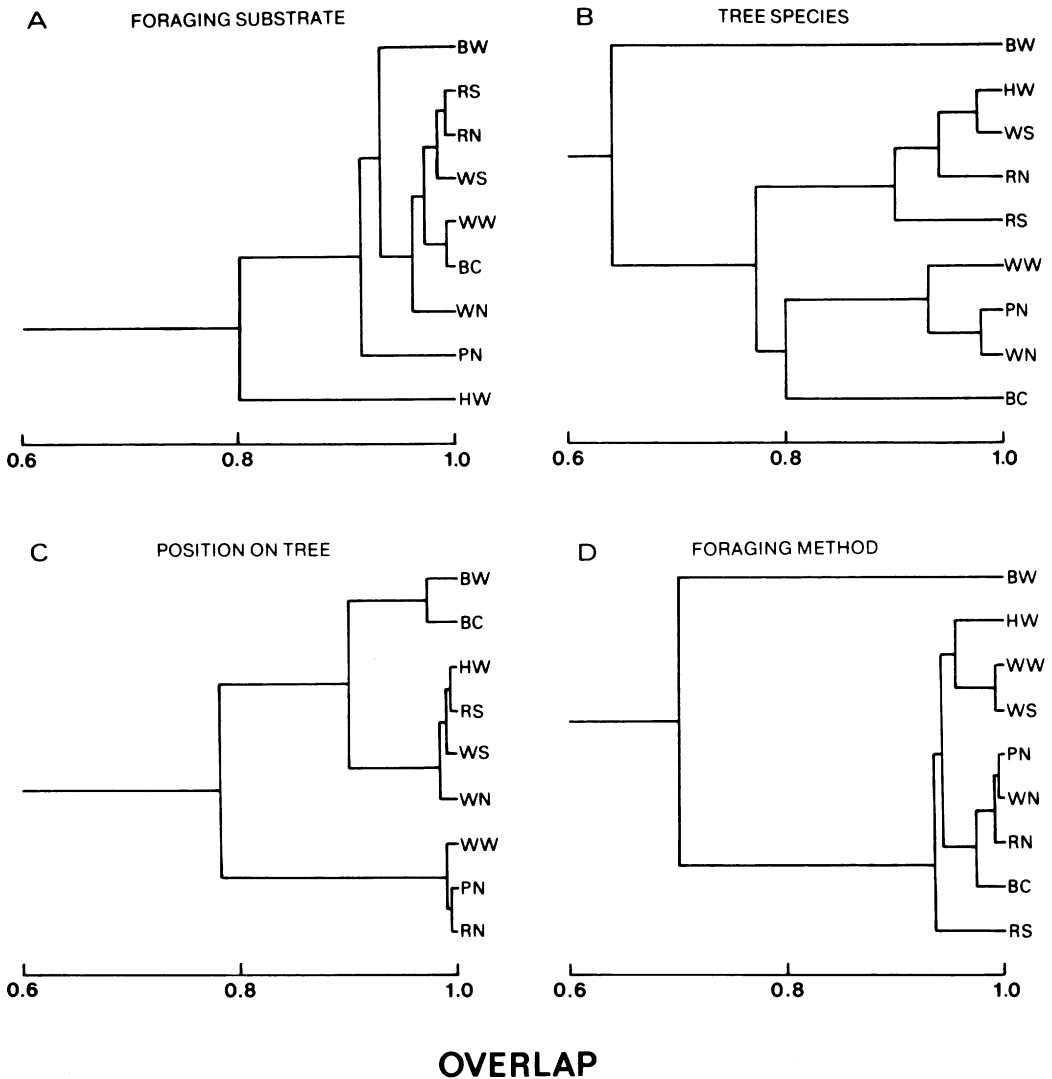


Fig. 17. Dendrograms showing interspecific foraging overlaps for: (A) foraging substrate, (B) tree species, (C) position on tree, (D) foraging method. See Table 19 for categories used in each analysis and Table 1 for bird name codes.

*Foraging Position.*—For each observation of foraging on trees, we recorded the position of the bird as on the trunk, on the branch (live or dead), or in foliage (Table 19). These data were used to compute overlap values among all species (except Lewis' woodpecker) and to produce a dendrogram (Fig. 17). At overlap values near 0.80 there were 2 groups, separated primarily by use of foliage. At overlap values of 0.90, the nonfoliage group split

into 2 additional groups, one specializing on trunks (black-backed woodpecker and brown creeper) and one using both trunks and branches.

For each foraging observation, we also recorded the height of the bird on the tree. Foraging height was related to tree height ( $r = 0.66$ ,  $P < 0.05$ , all bird species pooled). To compare foraging heights among bird species we computed the ratio of tree height to foraging height for each

observation, and compared mean height ratios between all pairs of species using planned contrasts. Brown creepers and white-breasted nuthatches foraged from lower positions in trees ( $P < 0.05$ ). No significant differences were detected between any other pairs.

Thus, for most species, mean foraging height was a function of mean tree height. To examine the relationship of foraging height and tree height along the entire range of tree heights observed, rather than at the mean only, we computed the slope of the relationship between foraging height and tree height for each bird species using linear regression. The brown creeper, which flies down to the base of each tree and works its way up along the trunk, foraged at low heights regardless of tree height (Fig. 18). Then we found 2 groups with very similar regression lines: a group of 4 species whose slopes exceeded 0.5 (pygmy nuthatch through hairy woodpecker), and a group of 4 species with slopes  $< 0.5$  (Williamson's sapsucker through white-breasted nuthatch). Slope would equal 0.5 if foraging height was random within the bounds set by tree height. Birds within each group were less similar in foraging behavior and morphology than birds between groups. For example, the red-breasted and Williamson's sapsuckers were in different groups. They are closely related phylogenetically, they are similar morphologically, and they both glean bark surfaces for carpenter ants (*Camponotus* spp.) during the breeding season. The black-backed woodpecker and hairy woodpecker were in separate groups, but they are also very similar morphologically. They foraged most on dead trees and often drilled for prey rather than gleaned (Table 19). Pygmy and red-breasted nuthatches are similar in size, and they foraged primarily on branches and in foliage (Table 19). The white-headed woodpecker and white-breasted nuthatch were not so clearly associated with members of either group or with each other, but they were similar in feeding on trunks instead of branches or foliage (Table 19). The white-headed woodpecker appeared

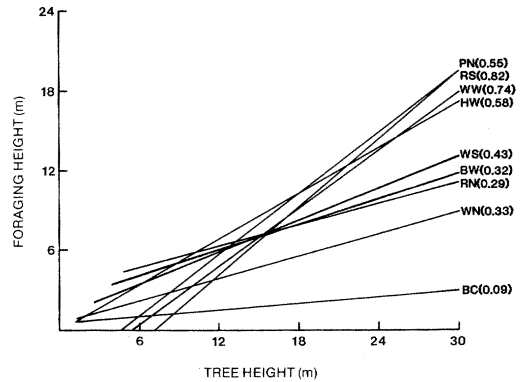


Fig. 18. Regression lines describing foraging height of bird species in relation to tree height. Numbers in parentheses are regression slopes. See Table 1 for bird name codes.

to use foliage more heavily than did the nuthatch, however.

Using the overlap values calculated from the tree position data we computed mean overlap among members within each group and between pairs across groups. Average overlap of birds within groups was less than that between pairs across groups, as expected. The mean overlap within groups was 0.85 and that across groups was 0.95. Although this difference was small, it appears that pairs most likely to overlap in position were more likely to forage at different heights within trees.

These results suggest that trees  $> 15$  m tall must be available in each stand to permit the vertical stratification of these cavity-nesters. If the patterns we have observed resulted from behavioral interactions between these pairs, availability of taller trees would reduce inter-specific aggression and perhaps increase nesting success.

**Foraging Method.**—We recorded the method of foraging used at each observation as gleaning, drilling, flycatching, or sapsucking (including phloem feeding) (Table 19). The black-backed woodpecker and hairy woodpecker were the only species that drilled more than 20% of the time. Most species gleaned during 80% or more of the observations, and the 3 nut-



Table 21. Niche breadth (on the diagonal) and overlap values<sup>a</sup> (below the diagonal) for 9 species of cavity-nesting birds. Values were calculated from all possible combinations of foraging substrate and behavior.

Bird <sup>b</sup>	BW	HW	RS	WW	WS	PN	RN	WN	BC
BW	0.076								
HW	0.060	0.319							
RS	0.017	0.301	0.172						
WW	0.000	0.289	0.170	0.121					
WS	0.069	0.247	0.342	0.212	0.181				
PN	0.000	0.111	0.163	0.356	0.118	0.078			
RN	0.037	0.162	0.169	0.191	0.206	0.350	0.130		
WN	0.020	0.312	0.280	0.455	0.260	0.476	0.314	0.137	
BC	0.000	0.168	0.206	0.230	0.265	0.264	0.131	0.441	0.047

<sup>a</sup> Overlap values range from 0 (no similarity) to 1.000 (perfect similarity).  
<sup>b</sup> See Table 1 for bird name codes.

hatches gleaned on over 90% of the observed occasions. Flycatching was important for Lewis' woodpeckers (76%) and red-breasted sapsuckers (10%). As shown by cluster analysis (Fig. 17), the black-backed woodpecker was isolated from the other species because of its higher proportion of drilling behavior. The red-breasted sapsucker also was isolated by its high proportion of sapsucking. At overlap values of 0.95 there were 2 groups, separated on the basis of gleaning vs. drilling. The nuthatch-creeper group gleaned over 90% of the time. The woodpecker-sapsucker group gleaned less of the time and drilled more.

*Multivariate Analysis.*—To examine the simultaneous influence of the behavioral and substrate variables described above, we used the categorical data to compute niche overlaps considering all combinations of values of variables. May (1975) recommended measuring the multidimensional resource use of a species rather than estimating this value by averaging or multiplying single dimension overlaps. Accordingly, we used all possible combinations of 6 variables in the overlap analysis: foraging height (4 classes), tree diameter (5 classes), substrate (6 classes), tree species (5 classes), position on tree (3 classes, live and dead branches not separated), and foraging method (4 classes). Of 7,200 possible combinations of these categories or resource states, 238 were actually used by the birds. We used

this matrix of 238 resource states and 9 bird species (Lewis' woodpecker excluded) to compute niche breadths and overlap values among all bird species (Colwell and Futuyma 1971; eqs. 2, 23). Niche breadth was widest for the hairy woodpecker and narrowest for the brown creeper (Table 21). There were more resource states possible (238) than the maximum number of observations of any 1 species (209). Thus, it is possible that these estimates underestimate niche breadth in some cases because of small sample size. Overlap values also were subject to limitations of sample size, but examination of Table 21 suggests that any inaccuracies were minor. For example, brown creepers and black-backed woodpeckers both were represented by fewer than 40 observations. But brown creepers had moderately high overlap with most other species, and black-backed woodpeckers had little overlap.

We used the overlap matrix of Table 21 to produce a dendrogram to examine foraging similarities among the species. There were 3 groups, which separated at an overlap value of 0.21 (Fig. 19). The black-backed woodpecker probably was isolated because it did the most drilling. Of the 2 other groups, one contained the sapsuckers and the hairy woodpecker and the other contained the 3 nuthatches, the brown creeper, and the white-headed woodpecker. In its overall foraging pattern, this latter woodpecker was more similar to a nut-

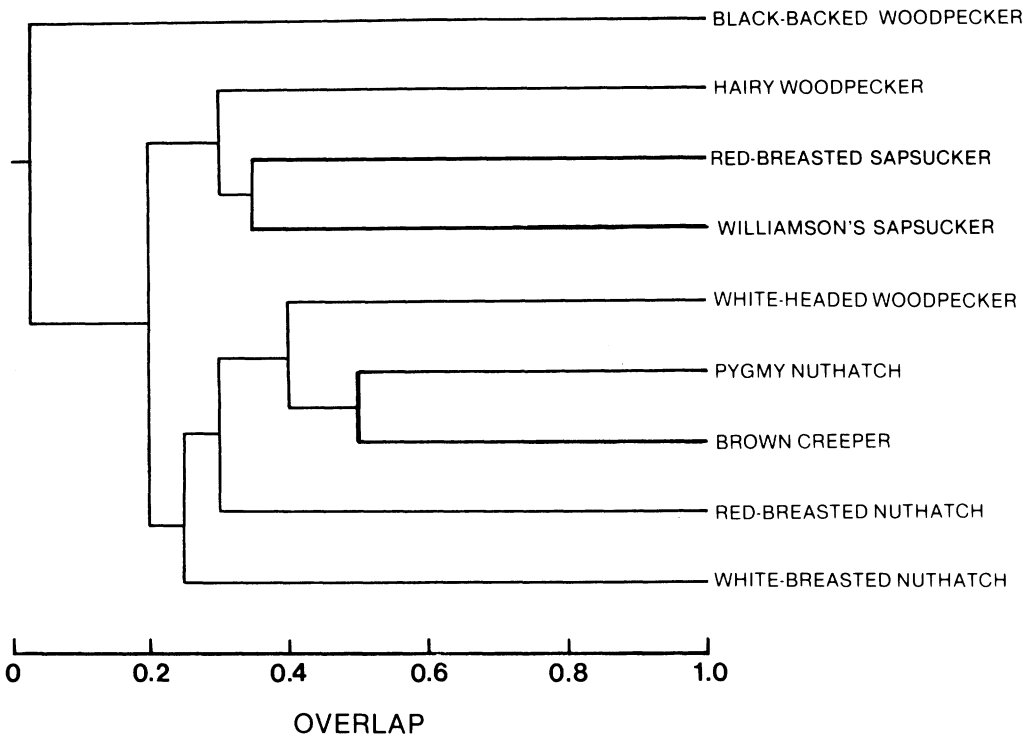


Fig. 19. Dendrogram showing results of cluster analysis based on multivariate foraging niche overlaps among birds (see text).

hatch than to the other woodpeckers (Fig. 17).

To determine if overlaps among birds on any subset of the 6 behavioral or substrate variables could be used to predict the multidimensional overlap matrix, we entered these 6 overlap values for each bird pair as independent variables in a stepwise multiple regression with the multidimensional overlap value of the same pair as the dependent variable. The independent variable most correlated with the multidimensional overlap was foraging method overlap ( $r = 0.75$ ,  $P < 0.0001$ ). The next variable to enter was tree species overlap. Together, these 2 variables explained 62% of the variation in total overlap. With all 6 variables in the equation, foraging method was the only variable significantly correlated with total overlap. Because the black-backed woodpecker overlapped so little with any other species (Table 19; Figs. 17, 19), we repeated the

analysis without this bird to see if correlations of overlaps among the remaining bird species remained similar. This time, foraging method still was most highly correlated with total overlap, but foraging position contributed significantly to the correlation as well, even when all variables were included in the equation. The explained variance was lower; foraging method and position now explained only 38% of total overlap variance. These analyses suggested that behavioral mechanisms were more responsible than differences in microhabitat for the foraging segregation of these birds.

*Discriminant Analysis of Snags with and without Feeding Sign.*—The preceding analysis emphasized interspecific comparisons of foraging behavior and foraging sites. Discriminant analysis comparing characteristics of those snags on the study plots with evidence of feeding to those without provided an examination of

Table 22. Results of discriminant analysis comparing snags with feeding sign to those without.

Variable	Means, pooled over all plots		Univariate F ratio	Entry step <sup>a</sup>	Significance as dis- criminator <sup>b</sup>	Correlation with dis- criminant score
	Without feeding sign N = 407	With feeding sign N = 725				
Diameter (cm)	24.5	32.6	80.84**	2	0.000	0.53
Height (m)	8.8	7.9	4.49*	6	0.000	-0.13
Top (presence or absence)	0.58	0.32	79.42**	5	0.003	-0.53
Foliage-bearing twigs (presence or absence)	0.17	0.21	2.40	7	0.038	0.09
White fir	0.15	0.43	97.91**	3	0.000	0.58
Red fir	0.35	0.07	164.63**	1	0.000	-0.73
Jeffrey pine	0.23	0.23	0.01	9	0.469	-0.01
Lodgepole pine	0.25	0.26	0.03	8	0.131	0.01
Bark cover (proportion) <sup>c</sup>	0.25	0.58	91.14**	4	0.000	0.56

<sup>a</sup> Order in which variables entered in stepwise analysis. First variables to enter were most powerful discriminators.  
<sup>b</sup> Probability that variable does not contribute to discrimination between groups, given the variables already entered into the discriminant function. Measured using change in Rao's V (Klecka 1975).  
<sup>c</sup> Analysis performed using arcsine transformation.  
\*  $P < 0.05$ .  
\*\*  $P < 0.005$ .

differences between snags used for feeding and those that were not. Results of this analysis apply only to snags on which birds drilled for prey because gleaning did not leave evidence of use. The black-backed and hairy woodpeckers drilled most often, and they also were the most dependent on snags for foraging. Because black-backed woodpeckers were scarce in the study area relative to hairy woodpeckers, this analysis most strongly reflected hairy woodpecker feeding preferences.

Of the 1,132 snags on the study plots, 725 showed evidence of feeding. We compared these to the 407 snags without feeding sign using diameter, height, top presence, foliage-bearing twig presence, bark cover, and species as independent variables. Snags with feeding sign were larger in diameter, were slightly shorter, were more often broken-topped, had more bark, usually were white fir, and rarely were red fir (Table 22). Foliage-bearing twig presence and amount of use of pine did not differ between forage and nonforage snags. Discriminant analysis using all variables showed that fir species and diameter were the best multivariate discriminators between forage and nonforage snags, followed by bark, top, and height. The correlations of each variable with the dis-

criminant scores showed that the 2 fir species, bark, and diameter were most strongly associated with the scores (Table 22).

This analysis demonstrated that forage snags were statistically different from nonforage snags on the basis of the snag characteristics we included, but the discrimination was weak. Only 24% of total variation was explained by separation of the 2 groups. The discriminant function correctly classified the snags into forage or nonforage categories 75% of the time. Approximately a third of the snags that did not have feeding sign were misclassified as forage snags, and a fifth of the snags with feeding sign were misclassified as nonforage snags.

These results reinforced some aspects of the analysis based upon the bird observations and contradicted others. The larger diameter of forage snags was evident in both analyses, possibly because of the energy considerations discussed earlier. The analysis of bird observations showed no foraging preferences for snag species (Fig. 16). The discriminant analysis, however, showed that there were significant differences in proportions of red and white fir used for foraging. The observation data included trees used by all bird species and

all foraging methods, whereas the snag analysis included only drilling and was weighted heavily by the hairy woodpecker. We observed drilling behavior on only 42 snags. This sample was small compared to the 725 snags on the plots with evidence of feeding. In addition, we recorded foraging observations only during spring and summer in 2 years, but snags on the study plots could have been fed upon at any time of the year and over a number of years. For these reasons, we believe that the forage vs. nonforage snag analysis provided a better measure of characteristics of drilling sites than the foraging observations.

We considered some variables in the snag analyses (top presence, foliage-bearing twig presence, and bark cover) that we did not measure during the bird observations. Of these, top presence and bark cover were good discriminators between forage and nonforage snags. Forage snags more often were broken-topped. Snags dead long enough to lose tops have been shown to attract more insects (Blackman and Stage 1924, Tanner 1942), especially larvae of cerambycid and buprestid beetles, which woodpeckers must excavate from under bark or from sapwood. Trees dead long enough to lose tops have been exposed to woodpeckers for more years and accumulate feeding sign over a longer period.

Bark cover was greater on forage snags (Table 22). Many more arthropods reside between bark and sapwood and in bark compared to wood tissues. It is likely that snags without bark support fewer arthropods than snags with bark and are less likely to be used for feeding. But snags without bark may have been used for feeding while the bark was present; feeding sign may have fallen with the bark.

### Snag Population Dynamics

**Falling Rate.**—Although we counted all snags on each study plot every year to record those that fell, we did not know the year of tree death for most snags. However, all snags on the Burned study plot

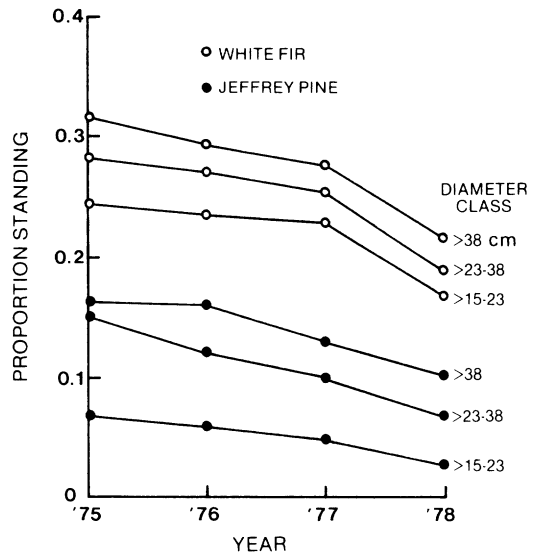


Fig. 20. Estimated proportion of trees killed by fire in 1960 still standing in years 1975 through 1978, by tree species and diameter class.

were killed in the 1960 Donner fire. We estimated the original number of standing trees by randomly selecting 10 subplots 30 m on a side and counting (by diameter class and species) all down trees originally rooted within each subplot. We added these to the number of snags recorded in 1975, and each year we recounted the snags and recorded all losses.

We calculated that there were 2,111 snags on the plot (250/ha) in 1960. In 1975 there were 400 snags (47/ha), a loss of 81% in 15 years. By 1978 there were 235 snags (28/ha), a loss of 89%. Jeffrey pine snags fell sooner than white fir snags, and small diameter snags fell sooner than larger diameter snags (Fig. 20). To compare falling rates, we computed the expected year by which 75% of the snags should have fallen for each size class using curves from Keen (1955). Differences among size classes within each species were slight except for the smallest Jeffrey pine class. Species differences were marked. It would have taken 16 years for 75% of the white fir snags to have fallen, but only 11 years for 75% of the Jeffrey pines to have fallen (excluding the smallest size).

Table 23. Cause of death of 204 new snags recorded on 6 study plots in 1978.

Cause of death	Plot						Totals
	Sagehen Creek snag plot	Jackass	Prosser	Unburned	Goshawk	Independence	
Insects		4	11	38	26	5	84
Unknown		1	1	36	26	11	75
Flooding	15						15
Suppression				9	2		11
Poison						9	9
Girdling						4	4
Lightning						3	3
Fire			3				3
Totals	15	5	15	83	54	32	204

Other researchers (Dahms 1949, Keen 1955, Lyon 1977, Cline et al. 1980) also have reported that larger diameter trees stood longer. Cline et al. (1980), for example, suggested that Douglas-fir snags >48 cm stood 4 times longer than those <8 cm. It is likely that the largest diameter trees will stand much longer than we estimate here. Unfortunately, our sample sizes for very large diameter trees were too small to permit a more detailed analysis.

Jeffrey pine snags were significantly taller on average than white fir snags, primarily because the tops of white firs break off more rapidly. On the study plots 83% of white fir snags had broken tops vs. 47% of Jeffrey pine snags. In addition, on the Burned plot the proportion of snags of all species with intact tops was greater among snags that had fallen than among those yet standing (0.18 vs. 0.07,  $t = 3.60$ ,  $P < 0.001$ ). Apparently a Jeffrey pine snag with an intact top has a higher center of gravity and is more susceptible to windthrow than a broken-topped white fir snag.

**Snag Recruitment.**—In 1978 we found 204 snags on 6 study plots from trees that had died since the 1977 counts. Insects killed most of these trees (Table 23). The Goshawk and Unburned plots had enough new snags ( $N = 137$ ) to merit comparisons of size and species with a point-quarter sample of 384 live trees on the same 2 plots (Table 24). The array of diameters among the new snags resembled that

among these live trees, except that more trees with dbh >23–38 cm were killed than would be expected if death was independent of diameter (Table 24). Fewer white fir and more Jeffrey pine were killed than occurred in the living-tree sample. Most of the Jeffrey pines were killed by the Jeffrey pine beetle. Trees were pre-disposed to this beetle by the 1977 drought, and mortality was widespread throughout the Sierra in 1978 (California Forest Pest Action Control Council 1978). It is likely, therefore, that the 1978 tree kill was considerably higher than usual, a result of exceptionally low rainfall.

Table 24. Species and diameter of snags killed in 1977–78 on Goshawk and Unburned plots compared to random sample<sup>a</sup> of live trees.

Category	Sample size	Percent observed (O)	Percent expected (E) <sup>a</sup>	Difference (O – E)
Tree species				
White fir	39	31.5	50.2	–18.7*
Red fir	12	9.7	8.9	0.8
Jeffrey pine	66	53.2	38.9	14.3*
Lodgepole pine	7	5.6	2.0	3.6
Diameter class (dbh, cm)				
>15–23	40	32.3	31.4	0.9
>23–38	57	46.0	35.9	10.1*
>38–53	16	12.9	18.2	– 5.3
>53	11	8.9	14.4	– 5.5

<sup>a</sup> Based on point-quarter analysis of 192 trees on each plot.  
\* Significantly different from 0.0 (binomial test, family error rate controlled at  $P < 0.05$  for 4 comparisons).

Table 25. Percent increase in standing crop of snags on Goshawk and Unburned study plots from 1977 to 1978 by diameter and species.

Diameter class (dbh, cm)	Tree species				Total	
	White fir	Red fir	Jeffrey pine	Lodgepole pine	%	N <sup>a</sup>
>15–23	36	–10	56	200	44	30
>23–38	140	129	83	60	98	55
>38–53	113	20	63	–100	64	14
>53	49	13	25	0	17	10
Total %	49	33	61	75	53	
N <sup>a</sup>	36	10	57	6		109

<sup>a</sup> Recruitment minus losses in each category.

This burst of new snags produced a 53% net increase of snags on the 2 plots (Table 25). Snags with dbh of >23–53 cm of both pine species increased most in proportion to the numbers already present. We then combined the 2 smallest diameter classes ( $\leq 38$  cm) and the 2 larger classes ( $> 38$  cm). Comparisons between white fir and Jeffrey pine showed that snag densities in each of these combined diameter classes should be similar in 15 years using the rates of fall that we calculated for the Burned plot from 1960–75 (Fig. 21). Most new snags were Jeffrey pine in 1978, but the majority of snags probably will be white fir after 15 years because Jeffrey pines should fall at a faster rate. This projection assumes that there will be no other sudden pulses of new snags during that period. Similarly, the relative number of small diameter trees should decrease compared to large trees.

White fir snags  $> 38$  cm dbh were preferred for nesting by most cavity-nesting bird species, and the number of these snags increased by 33% in 1978 over all plots. These preferred snags should provide more nesting opportunities for cavity-nesting birds once they decay sufficiently. The foraging studies showed no bird preferences for snag species, but did show preferences for snags  $> 23$ –53 cm dbh. There were 87% more snags of this size in 1978, and 50% of these already had evidence of feeding at the time they were counted. Hairy woodpeckers, black-backed wood-

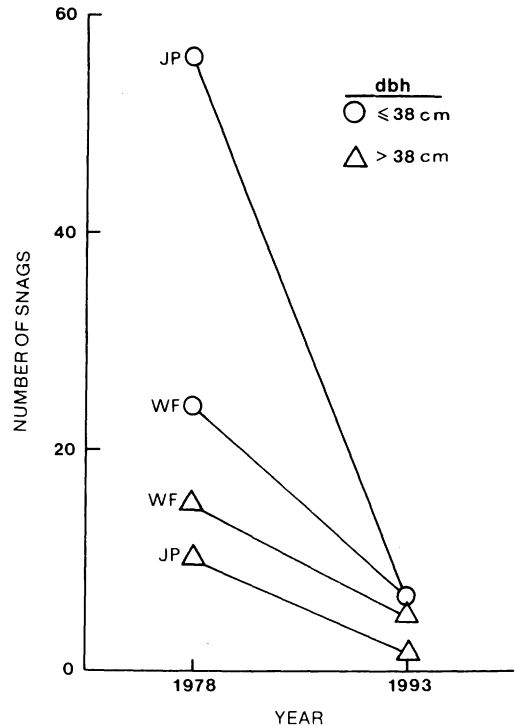


Fig. 21. Projected rate of fall of new (1978 mortality) snags of white fir (WF) and Jeffrey pine (JP) on Goshawk and Unburned plots from 1978 through 1993 by diameter class.

peckers, and other species were attracted immediately to Jeffrey pine beetles and other arthropods in these new snags.

### Cavity Nesting Bird Population Trends

*Bird Density Relative to Snag Density.*—To measure breeding densities of cavity-nesting birds in relation to snag density, we first compared breeding bird densities before and after snag removal on the Brush plot. Second, we compared bird populations among all plots to relate breeding bird density and diversity to snag density, snag diversity, and other vegetation characteristics on the plots. Third, we examined changes in bird density on the Burned plot as snags fell due to natural processes.

Beaver (1972) established the Brush plot and estimated the breeding bird popula-

Table 26. Comparison of breeding bird densities (pairs/40 ha) on the Brush plot before and after removal of all snags.

Bird species	Before snag removal 1969–70 <sup>a</sup>	After snag removal 1975–76 <sup>b</sup>
Northern flicker <sup>c</sup>	2	1
Mountain chickadee <sup>c</sup>	0	3
House wren <sup>c</sup>	3	0
Mountain bluebird <sup>c</sup>	12	0
Mountain quail	<1	0
Mourning dove	1	0
Common nighthawk	0	<1
Dusky flycatcher	17	18
American robin	2	1
Yellow warbler	7	19
Lazuli bunting	8	4
Green-tailed towhee	21	20
Dark-eyed junco	<1	3
Brewer's sparrow	10	4
Fox sparrow	66	55
Total pairs	149	128
Cavity-nesting pairs	17	4
Noncavity-nesting pairs	132	124
Cavity-nesting bird species diversity <sup>d</sup>	0.804	0.562
Percent change in cavity-nesting bird density		–76.5
Percent change in other bird density		–6.1

<sup>a</sup> Data from Beaver (1972).  
<sup>b</sup> Average density over 2 years.  
<sup>c</sup> Cavity-nesting species.  
<sup>d</sup> Shannon–Wiener index ( $H'$ ).

tion in 1969 and 1970, just before all snags were removed. Averaging the 2 years, he found 17 pairs of cavity-nesting birds and 149 pairs of other birds nesting on the plot (Table 26). Five years after snag removal, we found 77% fewer pairs of cavity-nesting birds, largely the result of the disappearance of mountain bluebirds. Pairs of noncavity-nesters declined by only 6% during this interval. Species diversity of cavity-nesting birds ( $H'$ ) declined 30%, from 0.80 to 0.56. Of 3 cavity-nesting species reported by Beaver (1972) before snag removal, only the northern flicker still bred on the plot after snag removal; one pair fledged 3 young from a nest in a 1.9-m stump remaining from a cut white fir snag. The mountain chickadee bred on the plot after snag removal, but apparently not during Beaver's (1972) study.

This species also nested in stumps remaining from cut snags.

Cavity-nesting bird populations on 6 other study plots varied from 19 to 65 pairs/40 ha in 1977 (Table 27). Although we censused each plot for 2–5 years, we have selected 1977 for interplot comparisons because bird densities were highest in that year on all plots, and resource limitation is more likely when birds are at their highest population densities.

We recorded 8 excavator species nesting in 1977: 2 plots supported 6 species, 2 plots had 5 species, 1 plot had 4 species, and 1 plot had only 1 species (Table 27). The most common excavator was the red-breasted nuthatch, except on the Burned plot where it was replaced by the pygmy nuthatch. The Williamson's sapsucker was the most consistently abundant woodpecker on most plots, but northern flickers were more abundant on the Burned plot than any other woodpecker on any plot. Lewis' woodpeckers were locally common, but none bred on any study plot. Pileated woodpeckers, rare in the basin, were observed once on the Unburned plot, but we could not establish that they bred in the vicinity during this study.

The 5 nonexcavating cavity-nesting birds were more uniformly distributed among the plots. The mountain chickadee and white-breasted nuthatch were found on all plots. Brown creepers bred on all but the Burned plot. House wrens and mountain bluebirds bred only on the Burned plot (Table 27). The average ratio of excavators to nonexcavators on all plots was 0.38, a value much lower than the 0.61 calculated by Jackman (1974) for 61 forest habitats in North America. This difference may reflect our classification of the abundant mountain chickadee as a nonexcavator instead of an excavator. Cavity-nesting bird density averaged 30% of total bird density on the plots, a value similar to that found by Jackman (1974).

Because cavity-nesting birds preferred snags >23 cm dbh for feeding and >38 cm dbh for nesting, we compared bird populations on the study plots to densities of snags in these classes as well as to vari-

Table 27. Cavity-nesting bird density (pairs/40 ha) on 6 study plots in 1977.

Species	Plot					
	Burned <sup>a</sup>	Unburned	Goshawk	Independence	Jackass	Prosser
<b>Excavators</b>						
Northern flicker	6.0	0.2	0.2	0.2	1.2	0
Williamson's sapsucker	0.2	3.6	2.4	2.4	0	0
Red-breasted sapsucker	0	0	0.2	0	0	0
Hairy woodpecker	1.2	1.2	0.2	0.2	2.4	0
Black-backed woodpecker	0	0.2	0.2	0.2	0	0
White-headed woodpecker	0	0	0	0	0.2	1.2
Red-breasted nuthatch	0	10.8	12.0	3.6	3.6	0
Pygmy nuthatch	10.8	0	0	4.8	4.8	0
<b>Nonexcavators</b>						
Mountain chickadee	26.3	21.5	21.5	15.6	15.6	13.2
White-breasted nuthatch	4.8	3.6	0.2	4.8	4.8	3.6
Brown creeper	0	8.4	9.6	4.8	4.8	1.2
House wren	4.8	0	0	0	0	0
Mountain bluebird	10.8	0	0	0	0	0
Excavator subtotal (A)	18	16	15	7	12	1
Nonexcavator subtotal (B)	47	34	31	25	25	18
Total cavity-nesters (A + B)	65	50	46	32	37	19
Other birds <sup>a</sup>	98	80	95	88	128	66
Total	163	130	141	120	165	85
Cavity-nesting bird diversity ( $H'$ )	1.66	1.54	1.32	1.47	1.70	0.92

<sup>a</sup> See Raphael (1980) for full list of species and description of study plots.

ables describing live tree and brush characteristics on the plots (Table 28). Both excavator and nonexcavator densities were strongly correlated with density of snags

>23 cm dbh. When this snag category was divided into large (>38 cm) and medium snags (>23–38 cm), excavators were more highly correlated with large snags, but

Table 28. Correlations<sup>a</sup> of cavity-nesting and noncavity-nesting bird density and diversity with plot vegetation variables on 7 study plots.<sup>b</sup>

Variable	Cavity-nesters				Noncavity-nesters	
	Excavators (A)	Nonexcavators (B)	Total (A + B)	Diversity <sup>c</sup>	Total	Diversity <sup>c</sup>
Snags >23 cm dbh/ha <sup>d</sup>	0.89*	0.98*	0.97*	0.74*	-0.28	0.56
Snags >38 cm dbh/ha <sup>d</sup>	0.86*	0.90*	0.90*	0.68*	-0.38	0.61
Snags >23–38 cm dbh/ha <sup>d</sup>	0.77*	0.92*	0.88*	0.64	0.12	0.34
Snag basal area <sup>d</sup>	0.83*	0.83*	0.85*	0.64	-0.38	0.60
Snag size diversity <sup>e</sup>	0.77*	0.68*	0.73*	0.77*	-0.43	0.90*
Heterogeneity index <sup>f</sup>	-0.45	-0.29	-0.36	-0.33	-0.46	0.13
Live tree basal area <sup>d</sup>	0.44	0.40	0.43	0.55	-0.59	0.87*
Live tree density	0.49	0.31	0.38	0.26	-0.53	0.55
Foliage height diversity	0.15	0.22	0.19	0.34	0.75*	0.79*
Percent brush cover	-0.34	-0.42	-0.40	-0.40	0.81*	-0.76*

<sup>a</sup> Pearson product-moment correlation coefficient.<sup>b</sup> Brush plot bird data is average of 1975 and 1976. All other bird data from 1977.<sup>c</sup> Bird species diversity ( $H'$ ).<sup>d</sup> Transformed using  $\ln(X + 1)$ .<sup>e</sup> Diversity ( $H'$ ) based on combination of 4 height classes and 5 diameter classes.<sup>f</sup> Coefficient of variation of point to tree distances (Roth 1976) as an index of horizontal patchiness.\* Values significantly different from 0 ( $P < 0.05$ ).



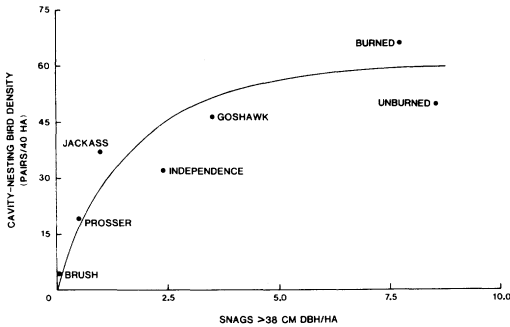


Fig. 22. Cavity nesting bird density (all species) in relation to density of snags >38 cm dbh on 7 study plots. Brush plot bird data are from average of 1975 and 1976 censuses; all other data are from 1977. The curve was fitted by eye.

nonexcavators were correlated equally with large and medium snags. We used partial correlation to test the relation of excavator density to total snag density, controlled for either large or medium snag density. When the effect of large snags was removed statistically, the partial correlation coefficient was low ( $r = 0.45$ ,  $P = 0.19$ ), but removing the effect of medium snags had little impact ( $r = 0.77$ ,  $P = 0.05$ ). Large snags were more closely associated with excavator density. Similar tests performed on nonexcavators showed significant correlations with both large and medium snags when controlling for either. The positive correlation of total cavity-nesting bird density and large snag density (Fig. 22) suggested that density of large diameter snags limited cavity-nesting bird density. This relationship was supported further by the correlation of nonexcavating cavity-nesting bird numbers with numbers of cavities available on the study plots (log transformed,  $r = 0.89$ ,  $P = 0.003$ , Fig. 23).

Both excavator and nonexcavator densities were significantly correlated with each of the snag variables but not with any of the live tree or brush variables (Table 28). Conversely, noncavity-nesting bird density was not correlated with any snag variable but was correlated with foliage height diversity and with percent brush cover. Cavity-nesting bird diversity was best correlated with snag size diversity

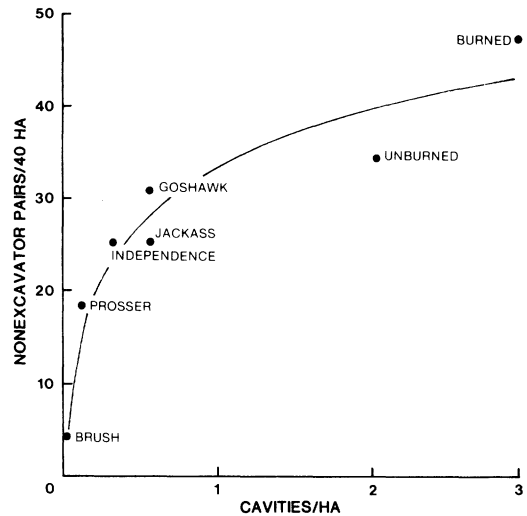


Fig. 23. Numbers of nonexcavating cavity-nesting birds in relation to cavity numbers on 7 study plots. Brush plot bird data are average of 1975 and 1976 censuses; all other data are from 1977. The curve was fitted by eye.

(Fig. 24) and with snag density (especially large snags).

Noncavity-nesting bird diversity was correlated with live tree basal area, foliage height diversity, brush cover, and, surprisingly, with snag diversity (Table 28). The correlation of cavity-nesting bird diversity with snag size diversity was anticipated; nesting studies showed significant interspecific differences in tree heights used for nesting. We did not anticipate a correlation of noncavity-nester diversity with snag diversity, and we cannot corroborate this result with other evidence, except that we observed birds preferentially singing from snags. We suspect either a spurious correlation resulting from confounding effects of other variables, or chance.

*Yearly Variation in Breeding Bird Density.*—The Burned and Unburned study plots had been censused periodically since 1966 (Bock and Lynch 1970, Bock et al. 1978, Table 27). From the 1960 Donner fire to 1978, the number of snags on the Burned plot decreased dramatically (Fig. 21). Using the falling pattern estimated by Keen (1955), we calculated that

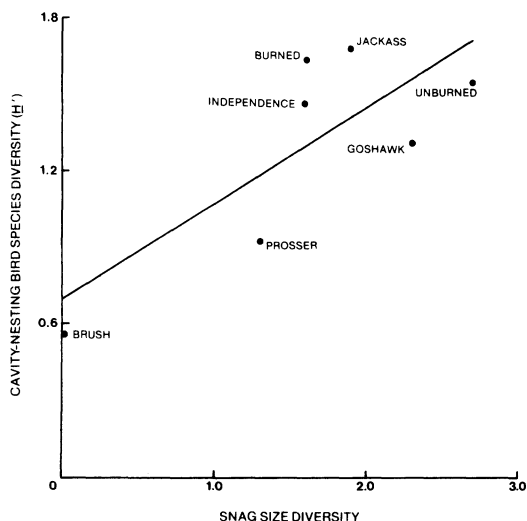


Fig. 24. Diversity of cavity-nesters ( $H'$ ) in relation to snag size diversity (20 combinations of snag height and diameter). Brush plot bird data are from average of 1975 and 1976 censuses; all other data are from 1977. The line is from a least squares regression ( $r = 0.89$ ).

80% of the snags present in 1960 probably were standing in 1966. By 1978 only 11% remained standing. Counting only snags >38 cm dbh (the size preferred for nesting and feeding), there were 33 snags/ha in 1966 and 6/ha in 1978. We expected that cavity-nesting bird numbers would decline over this period on the Burned plot and would remain constant on the Unburned plot because snag density probably was stable over time on the latter (tree mortality matched falling snags). However, no decline was apparent on either plot (Fig. 25). Both excavators and nonexcavators reached their highest densities in 1977. The comparisons of bird populations on all plots (Table 27, Fig. 22) implied that cavity-nesting bird density was limited by large snag (>38 cm dbh) density when there were 7.5 or fewer stems/ha. We expected to have found years of higher bird density on the Burned plot prior to 1977 when snag density was >7.5 stems/ha. Such was not the case. We hypothesize that cavity-nesting bird densities were limited by availability of large snags up to snag densities of about 7.5

Table 29. Difference in bird density (pairs/40 ha) between study plots (Burned minus Unburned) over time. Bird data for 1966–68 from Bock and Lynch (1970), for 1975 from Bock et al. (1978), and for 1976–79 for this study.

Year	Bird group		
	Excavators	Nonexcavators	Noncavity-nesters
1966	6.2	5.1	-13.4
1967	2.0	5.8	-2.1
1968	8.2	11.8	-22.1
1975	0	7.0	-4.9
1976	0.8	6.8	-12.3
1977	1.9	13.1	17.5
1978	1.0	7.1	35.5
1979	-0.3	2.7	18.7

stems/ha and were limited by other factors when snag densities were above that level.

This hypothesis predicted that cavity-nesting bird numbers would decline on the Burned plot after 1978 as snags continued to fall. To test this prediction, we censused birds on both plots in 1979. Bird densities declined slightly (Fig. 25). For the first time, however, excavator density on the Burned plot dropped below that on the Unburned plot (Table 29). Excavator densities were higher on the Burned plot than on the Unburned plot in 1966–68, but were nearly identical on the 2 plots from 1975–78. During this same period, nonexcavator densities remained higher on the Burned plot (Table 29), but in 1979 nonexcavator density was more similar on the 2 plots than in any previous year. Large snag density was slightly lower in 1979 (0.8 fewer stems/ha) on the Burned plot than on the Unburned plot, which may explain the convergence of bird densities on the plots. Even though all these differences were small, they were in the predicted direction and supported the suggestion that snag numbers limit cavity-nesting birds.

Although snag density might determine a maximum density of cavity-nesting birds, it was apparent that yearly densities fluctuated below this maximum as evidenced in particular by the exceptionally high bird density found in 1977. The preceding 12-month period was marked by

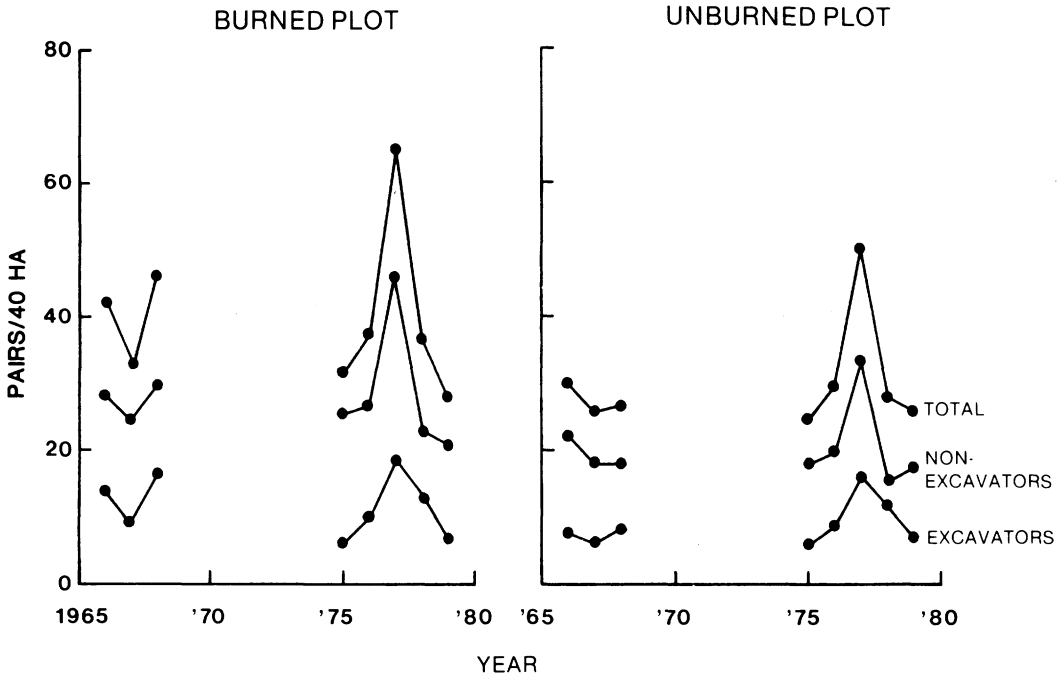


Fig. 25. Yearly variations in cavity-nesting bird density on Burned and Unburned study plots. Data from 1966–68 are from Bock and Lynch (1970); 1975 data are from Bock et al. (1978).

extremely low precipitation, which suggested that yearly density might somehow be correlated with precipitation. To examine such a relationship, we computed a regression of cavity-nesting bird density against total precipitation and found significant negative correlations on both plots. Variation in precipitation (log transformed) explained 83% of the yearly variation in total cavity-nesting bird density (sq root transformed) on the Burned plot ( $r = -0.91$ ,  $P < 0.001$ ) and 64% on the Unburned plot ( $r = -0.80$ ,  $P = 0.009$ ). There was no correlation between non-cavity-nesting bird density and precipitation on either plot ( $r = 0.14$ ,  $P = 0.365$  on Burned plot;  $r = 0.50$ ,  $P = 0.106$  on Unburned plot).

Weather factors apparently can hold these cavity-nesting bird populations below a maximum level set by snag density, territoriality, and other factors. Tramer (1969), Rotenberry (1978), and Rotenberry et al. (1979) discussed effects of weather

on bird communities and concluded that relative abundance (community evenness) should be more likely to change than species richness in variable environments. Cavity-nesting birds were affected by precipitation at Sagehen Creek, but noncavity-nesters were not. Cavity-nesting species tend to be resident whereas the majority of other birds are migratory (von Haartman 1968). In the Tahoe National Forest and Lake Tahoe basin, 77% of the 35 cavity-nesting species are resident in winter compared to 48% of the 124 non-cavity-nesting species (compiled from Winter 1974). Most cavity-nesters, then, are subject to the vagaries of winter whereas half of the noncavity-nesters migrate and escape the harsh and variable winter in the high Sierra.

Weather could affect bird numbers in a variety of ways, influencing mortality, immigration and emigration, migration, fecundity, prey numbers, and foraging, for example. We cannot confirm or reject any

of these possibilities, but circumstantial evidence suggested that changing fecundity was not the major factor. There would have been a lag effect such that populations would be affected the year following the climatic event. If the drought of 1976–77 had caused unusually high prey density as insects were attracted to dying trees, this high prey density could have allowed birds to raise larger broods and perhaps to have had a higher frequency of second broods. The number of fledged young would have increased, and if a constant proportion had survived over the winter, there would have been more breeding adults the following spring (1978). But the pulse of birds occurred in 1977, the spring immediately following the drought. We believe it was more likely that overwintering mortality was the variable most affected by weather (cf. Fretwell 1972, Graber and Graber 1979), or that weather influenced prey density or availability, which in turn influenced immigration into or emigration from the area (e.g., Crockett and Hansley 1978).

## MANAGEMENT IMPLICATIONS

### Snag Characteristics

*Size.*—The discriminant analysis comparing nest and non-nest snags (Table 15) showed that nest snags were larger in diameter and that snag diameter was the most important discriminator between the 2 groups. Larger diameter snags allow space for excavation of larger diameter cavities, and clutch size of hole-nesting passerines has been shown to increase with increased cavity diameter (Karlsson and Nilsson 1977). Additionally, larger diameter trees provide thicker insulation around the nest cavity. O'Connor (1978) found that the mean date of egg laying of female great tits (*Parus major*) roosting in well-insulated, warmer nest boxes was earlier than for females roosting in less-insulated, cooler boxes. Earlier laying can be advantageous; more time is available to feed young, and fledging success might increase as a result (Cody 1966). Klopfer

(1963, 1965) postulated an innate (genetic) component in the habitat preference of the chipping sparrow, which can be modified by experience. Hilden (1965) argued that inheritance plays a primary role in habitat selection.

Natural selection should favor birds choosing larger diameter nest trees. Bull (1978) and Thomas et al. (1979) recommended managing for snag diameters equal to or greater than the smallest diameter known to be used by each excavator. We favor the approach of Conner (1979) and recommend managing for mean diameter, which varied from 43 cm for hairy woodpeckers to 84 cm for red-breasted sapsuckers in our study (Table 30). If management for mean diameter is not possible because of other constraints, an intermediate diameter can be selected, such as the thirty-third percentile of the nest tree diameter distribution (Table 30). Providing enough large snags will be possible in many intensively managed forests only if selected trees and stands are maintained beyond the usual rotation age, or if patches of old-growth forest are retained.

For foraging, cavity-nesting birds preferred trees with dbh of >25–53 cm, especially trees of >38–53 cm. Trees of this size provide an optimum combination of high foraging surface area and low inter-tree flight distance such that net energy intake is maximum (Krebs 1978). All birds except pygmy nuthatches, red-breasted nuthatches (which fed in live foliage), and brown creepers fed in snags more than we predicted based upon snag availability (Table 20), even when snags were scarce (Fig. 13). Managers should leave trees and snags >38 cm dbh whenever possible. They provide feeding and nesting habitats for these birds that are nearly irreplaceable under modern forest harvest procedures.

These bird species segregated themselves for nesting in snags on the basis of height. We found a positive correlation between snag size diversity and cavity-nesting bird species diversity on the study plots (Fig. 24). Management for a diver-

Table 30. Characteristics of excavator and brown creeper nest trees in pine–fir forests in the Sagehen Creek area.

Bird species <sup>a</sup>	Nest tree dbh (cm)		Nest tree height (m)		Nest tree species <sup>c</sup>		Tree condition <sup>c</sup>			Habitat use <sup>c</sup>	
	Mean	Min <sup>b</sup>	Mean	Min <sup>b</sup>	Fir	Pine	Live	Hard snag	Soft snag	Burned	Unburned
PN	46	38	6	5	XX					XX	
RN	71	53	15	12	X	X	X	X			XX
BW	46	41	17	13	X	X	X	X		X	X
HW	43	38	14	10	X	X			XX	X	X
NF	61	48	13	9	X	X			XX	X	X
LW	66	56	11	9	X	X			XX	XX	
WW	66	51	4	3		XX			XX	XX	
WS	81	69	20	16	X	X	X	X			XX
RS	84	66	20	17		XX	X	X			XX
BC	69	53	25	21		XX	X	X			XX

<sup>a</sup> See Table 1 for bird name codes.  
<sup>b</sup> Min = minimum size calculated using 33rd percentile of observed size distribution.  
<sup>c</sup> X = category used less than 60% of the time; XX = category used more than 60% of the time.

sity of snag heights among large diameter trees will meet more species' requirements. As with diameter, we recommend managing for mean rather than minimum heights (Table 30). Taller trees provide greater security against ground predators (Dixon 1927, Kilham 1971, Dunn 1977).

The way to assure diversity of snag heights is to maintain a mixture of snag species, diameters, and ages. Snag height decreases with time as tops break off. Firs break more quickly than pines. A mixture of the 2 snag species will likely contain both broken and intact trees. On any site, diameter and height are correlated and managing for diameter diversity will result in height diversity.

In general, it is best to manage for taller snags because tall snags become shorter with time (for an exception see Carroll 1895). Our observations of foraging heights of birds in relation to tree height (Fig. 18) suggest that taller trees may reduce inter-specific conflicts by allowing vertical segregation of foraging activity. Managing for taller snags will require longer rotations to produce taller live trees.

*Tree Species.*—At Sagehen Creek, white fir snags were preferred by birds for nesting, measured both in highest proportional use and greatest deviation from availability (Fig. 5). Red fir and Jeffrey pine snags were used proportionally less than predicted by nearly all bird species; lodgepole pine was used in proportions

similar to predicted. Preferences for tree species vary geographically. For example, northern flickers preferred aspen in Ontario (Lawrence 1967), Douglas-fir in British Columbia (Kelleher 1963), ponderosa pine in Oregon (E. Miller, unpubl. data), western larch in Montana (McClelland 1977), and white fir in California (this study). These excavators appear to be opportunistic over broad geographic areas, selecting tree species that provide the most suitable substrate (wood consistency, decay, etc.) for nest excavation in any particular locality.

For feeding, the birds we observed used all snag species in the same proportion as predicted by availability (Fig. 16). Among those birds feeding in live trees, Jeffrey pines were used more than predicted, and white fir and lodgepole pines were used less than predicted. In contrast, the discriminant analysis comparing snags with and without feeding sign (Table 22) showed an apparent preference by bark-drilling species for white fir snags.

Thus, white fir snags were favored by birds for both nesting and feeding. White firs stand longer than similar sized trees of other species (Fig. 21) so they provide potential habitat over a greater number of years. In Sierra Nevada mixed conifer forests, snag management should emphasize white fir but maintain a species mix similar to that occurring naturally to provide for birds preferring other tree species.

**Decay State.**—We described 6 tree decay states based upon tree condition (live or dead), branch structure, and other factors (Table 8). States 5 and 6 were soft snags, which usually were infected with wood rots, especially red belt fungus. Excavators have shown strong preferences for trees infected with heart-rot fungi and other decay organisms (Lawrence 1967, Shigo and Kilham 1968, McClelland and Frissell 1975, Conner et al. 1976, Jackson 1977). Of the snags we sampled, 66% were soft and these contained 73% of all nests in snags. Proportional use of decay states measured by pooling nests of all birds matched availability quite closely (Fig. 6). Nests of individual species, however, revealed marked interspecific differences. Excavators chose different decay states probably because of different morphological adaptations for feeding. Drillers (e.g., black-backed and hairy woodpeckers) nested in harder snags than nondrilling flickers and Lewis' woodpeckers, which excavated nests only in soft snags. That this group of species exploited all decay states suggests that natural selection has led to evolution of a variety of foraging behaviors and morphologies to minimize interspecific competition and to maximize individual fitness through more efficient resource utilization.

The optimum snag population to provide nesting and feeding habitat is a mixture of all snag decay states. To achieve such a mixture, snags must be recruited continuously. An even-aged population of snags will not provide suitable habitat for all species at 1 time, although a cohort of snags will be suitable for all species as it decays. Snags can be managed as an uneven-aged collection of individuals, or as small even-aged patches with interpatch age variation.

**Suitability Predictor.**—The discriminant analysis comparing nest and non-nest snags (Table 14) revealed that 3 variables contributed significantly to the differences between the 2 groups: snag diameter, bark cover, and top presence. Another discriminant analysis using only these 3 variables increased the classification error

by only 1%. The new discriminant equation can be used to create a nesting Snag Suitability Index (SSI), as follows:

$$SSI = 0.06 (D) + (B) - 0.52 (T) - 0.80$$

where  $(D)$  = snag dbh in centimeters,  $(B)$  = decimal proportion of stem covered by bark, and  $(T)$  = top, assigned a value of 1 if the top is intact, or 0 if broken. If the SSI value is positive, the snag is suitable for nesting. If the value is negative, it should be classified as unsuitable. The magnitude of the SSI of a snag is proportional to the probability of its suitability. Values ranging from  $-1.0$  to  $1.0$  indicate borderline snags that cannot be classified reliably.

**Snag Dispersion.**—Snag density requirements are best met by providing snags in dispersed clumps rather than as single trees uniformly scattered over an area. The discriminant analysis comparing stand characteristics of nest plots and random plots showed that the 2 best discriminators were number of snags  $>38$  cm dbh and number  $>23$ – $38$  cm dbh (Table 4). The average density of these snags surrounding nest sites of excavators was 4 times greater than that on the randomly distributed plots. Pairwise discriminant analyses between nest sites of each excavator and the random plots showed that snag density was a significant discriminator for all species except the red-breasted nuthatch (Table 5). Most birds preferred to nest in patches of snags.

The foraging studies suggested that closely spaced large trees ( $>38$  cm) allowed maximum energy intake, partly by reducing intertree flight time. Birds foraged on both live trees and snags, but birds foraging on snags tended to continue to select snags, as revealed by the substrate transition probability matrices (Table 20). Frequency of interclump flight is a function of clump size. Birds can forage within a large clump of snags for a relatively long period of time; small clumps will require frequent interclump flights. We suggest managing for 1 clump/2 ha composed of approximately 15 snags  $>23$  cm dbh.

Clumps composed of fewer stems should be closer together. Clump density should not, however, be lower than 1 clump/2 ha.

*Location.*—The edge between burned and unburned forest supported the greatest diversity of cavity-nesting birds (Table 3), followed by lodgepole-meadow and burned pine-fir. Burned pine-fir, lodgepole-meadow, and pine-fir supported the highest nest densities, but the proportion of nests in pine-fir forest was lower than predicted based on the amount of that type in the study area (Fig. 2). Burns and meadow edges were preferred nesting habitats. These types should be given priority in snag management plans.

### Snag Density

Density of cavity-nesters was limited partially by snag density (Table 28, Fig. 22). Bird density tended to increase in a nonlinear (convex) fashion with increasing snag density. Bird density increased rapidly as snag density increased from 0–3/ha (snags >38 cm dbh) and thereafter increased slowly to a maximum at 7.5 snags/ha. Bull (1978), Evans and Conner (1979), and Thomas et al. (1979) assumed a linear relationship between bird and snag density in their computations of snag requirements. If a convex curve represents a closer approximation, predictions of bird density assuming a linear relationship may underestimate potential bird populations, and snag requirement estimates based on linear relationships may be conservative (overestimated). Assuming it is better to err on the side of too many snags rather than too few, continued use of a linear relationship is reasonable.

Snag density changes as snags fall and live trees die. Snag population dynamics differ on burned and forested areas; only the latter areas have the potential for continuous snag recruitment. In addition, bird communities differ in burned and unburned forests.

*Burned Forest.*—In burned forests and in clearcuts where snags are retained, an initial density of snags declines over time

with little opportunity for snag replacement. These open forest types provide valuable habitat for cavity-nesting birds (Table 3). Removal of all snags from burned areas causes a drastic decline in cavity-nesting bird density (Table 26).

We have constructed a model that illustrates hypothetical changes in snag and bird density on a burned area after a fire (Fig. 26). Snag density is very high initially and far exceeds numbers required by cavity-nesting birds. When surplus snags are available, these birds probably are limited by their territorial behavior (Watson and Moss 1970, Krebs 1971, Verner 1975), but actual year-to-year bird densities fluctuate below this upper limit in response to weather (Fig. 26). Occasionally, favorable conditions allow the population to reach the ceiling set by territory size. Eventually, snag density declines enough to become limiting. As snags continue to fall, potential bird density also declines. Foresters should provide sufficient snags to maintain potential bird density at the ceiling set by territorial behavior.

Birds nesting in burns preferred soft snags (Figs. 3, 7). These trees generally had been dead 6 years or more, and probably were most valuable as nest sites 15–20 years after death. On the Burned study plot, only 33% of the initial number of firs and 16% of the pines were standing after 15 years (Fig. 20). Given these falling rates, 3 hard firs and 6 hard pines were required at year 1 to produce 1 standing soft snag of each species at year 15. If a management objective is to provide for 3 soft snags (e.g., 2 fir and 1 pine) at year 15, 12 hard snags (6 pine and 6 fir) must be left in the first year. Soft snags should be managed using these “Hard Snag Equivalents” (HSE), the number of hard snags necessary to produce 1 soft snag.

Hardin and Evans (1977), Bull (1978), Conner (1978), Evans and Conner (1979), and Thomas et al. (1979) calculated the number ( $Y$ ) of standing snags required to provide habitat for excavators using the formula:

$$(Y) = (A) \times (B) \times (C)$$

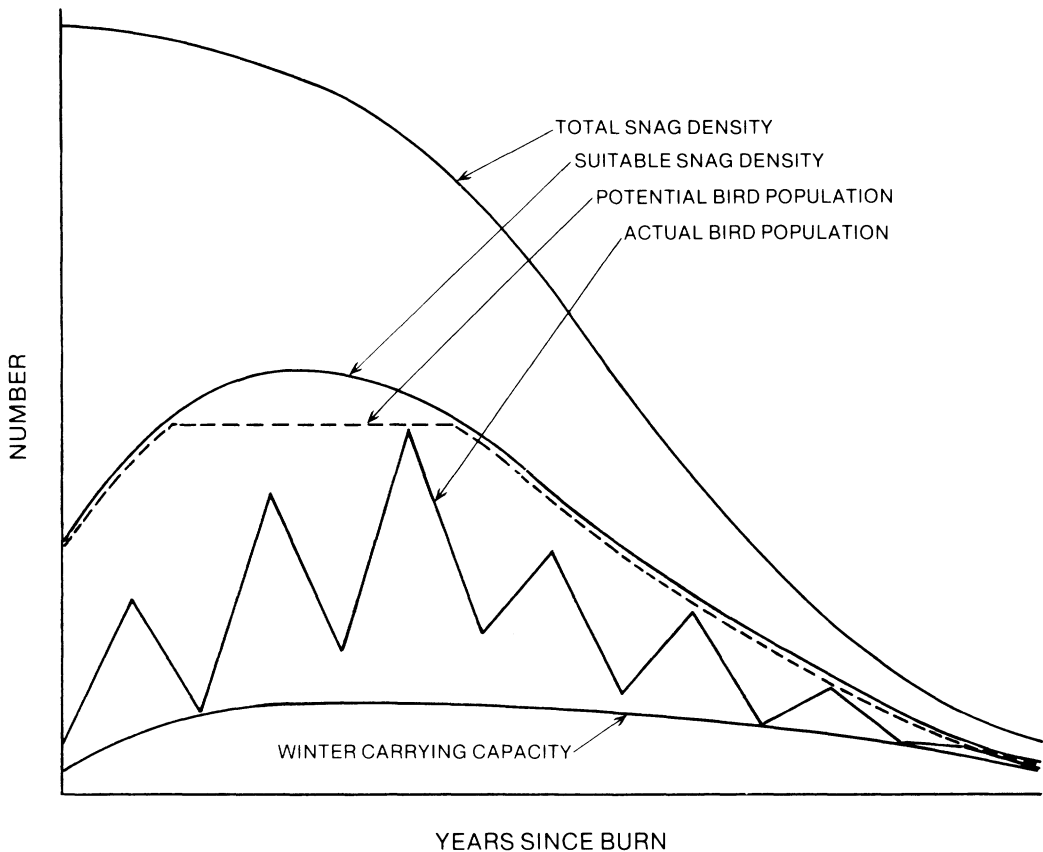


Fig. 26. Hypothetical model showing changes in cavity-nesting bird density and snag density over time on a burned forest. Actual yearly bird density fluctuates in relation to weather between extremes set by winter carrying capacity and snag density or territorial behavior. Number of suitable snags increases initially as snags decay, then declines as they fall. Potential bird numbers are limited initially by suitable snag density. During an intermediate period, when surplus snags are available, birds are limited by their territorial behavior. As snags continue falling, potential bird density is again limited by suitable snag density.

where (A) = maximum cavity-nesting bird density, (B) = number of snags used annually for nesting and roosting by each pair, and (C) = a reserve of suitable snags. Snag suitability should be estimated using a classification function such as our Snag Suitability Index (SSI) presented earlier. These suitability indices are not infallible; factors not included in the computations may cause a bird to reject a snag classified as suitable. Thus, a reserve is necessary to provide for unmeasured variables. Using the SSI from our studies, we found 3 suitable snags with no evidence of past nesting use for every 1 with such evidence. If Sagehen Creek is typical of Sierra Nevada

pine-fir forest, the snag reserve (C) should be set at 3.

The number (B) of nesting and roosting snags used by each pair and its young each year varies from 1 to 4 (Evans and Conner 1979). Including the snag reserve (C), each pair of birds should have 3–12 suitable snags available each year depending on the value of (B) for a particular species. These values correspond to 9–72 Hard Snag Equivalents (HSE). We counted 68 HSE/pair of excavators on the Burned study plot in 1977 (the year of highest bird density), which was within the calculated range and was the equivalent of 8 soft snags/ha.



Table 31. Recommended number of suitable snags required to support maximum densities of excavators and brown creepers in pine–fir forests in the Sierra Nevada.

Bird species	Maximum density (pairs/40 ha)	No. cavities excavated/ year <sup>a</sup>	Suitable snags required/40 ha		Source of maximum density estimate
			N <sup>b</sup>	HSE <sup>c</sup>	
Pygmy nuthatch	36	1	108	324	Pugh and Pugh 1957
Red-breasted nuthatch	12	1	36	36	Robert 1966
Black-backed woodpecker	0.5	4	6	6	Beaver 1972
Hairy woodpecker	16	4	192	768	(see text)
Northern flicker	12	1	36	108	Pugh and Pugh 1957
Lewis' woodpecker	12	1	36	108	assumed similar to northern flicker
White-headed woodpecker	5	3	45	270	Kilgore 1971
Williamson's sapsucker	2	1	6	6	Bock et al. 1978
Red-breasted sapsucker	2	1	6	6	Beaver 1972
Brown creeper	20	1	60	60	Akers 1975

<sup>a</sup> From Bull (1978) and Evans and Conner (1979).  
<sup>b</sup> N = number of snags.  
<sup>c</sup> HSE = number of hard snags required to produce desired number of soft snags.

A final point concerns the calculation of factor (A). Maximum bird density usually is calculated using minimum territory size, but we are not aware of any studies demonstrating a minimum territory size defended by any excavator. Territory sizes published in the literature are usually estimated by dividing an area by the number of pairs found in that area, by measuring distances between nests, or by mapping activity ranges. Territory sizes reported using these methods vary considerably, even among neighboring conspecifics (cf. Howell 1952). Until we have better information relating environmental and other factors to territory size (e.g., Schoener 1968), we cannot agree that maximum density should be calculated on the basis of assumed minimum territory size. Rather, we suggest simply using published records of maximum densities for each species.

We reviewed all breeding bird censuses on forested plots in California published in *American Birds* (Raphael and White 1978) and recorded maximum densities for the brown creeper and the excavators occurring at Sagehen Creek (Table 31). Estimated maximum densities of the same species, calculated from territory sizes, were reported by Bull (1978). Maximum hairy woodpecker density was 5 times greater in the censuses than predicted by

Bull (1978). Bull reported hairy woodpecker territory size to be 10 ha, but Lawrence (1967) reported 2 territories (=home range) averaging 3.5 ha. Bock (1979) found that hairy woodpeckers were most abundant in the northeastern part of North America (the site of Lawrence's study) and were relatively rare in the central Sierra of California. However, the maximum density in California was twice that predicted by using Lawrence's home range estimate (Table 31). Bock's geographical blocks were quite large, encompassing 5 degrees latitude and longitude. It is reasonable to expect pockets of high woodpecker density in favorable habitat within these large areas even though average density over the entire block is low. The maximum density reported in *American Birds* was 20 pairs/40 ha, a value more than 2 standard deviations above the mean of 16 censuses. We used only 16 pairs of hairy woodpeckers/40 ha (2 standard deviations above the mean) in our calculations (Table 31).

In contrast, maximum densities of the 2 sapsuckers in published censuses were lower by a factor of 5 compared to Bull's (1978) estimates. Minimum territory sizes reported for yellow-bellied or red-breasted sapsuckers in the literature varied from 0.6 ha (Howell 1952, in British Columbia) to 2.0 ha (Lawrence 1967, in Ontario). For

the Williamson's sapsucker, these minimum estimates ranged from 0.4 ha (Crockett 1975, in Colorado) to 0.8 ha (Young 1975, in New Mexico). Both the *American Bird* censuses and our censuses predicted a maximum of 2 pairs of each sapsucker on 40 ha. At 0.6 ha/territory, there could be 67 pairs on 40 ha. We suspect that this density is never found over a large area. Maximum density estimates should be based on censuses rather than on estimates of minimum territory sizes. We recommend using the *American Bird* census values for management purposes until more data become available.

Six excavator species nested in burned habitats at Sagehen Creek (Table 30). Maximum potential density of this group was 82 pairs/40 ha (Table 31), nearly 5 times larger than the maximum density (18 pairs/ha) we censused in any 1 year. Using the formula described earlier, we calculated a total snag requirement ( $Y$ ) of 423 suitable soft snags (1,578 Hard Snag Equivalents) to support the maximum calculated population on 40 ha. The Burned study plot contained 2,029 standing snags/40 ha in 1975, 15 years after the fire. The estimated snag requirement represented approximately one-fifth of this total. Managing for the maximum excavator population would require retaining at least 20% of the snags on this burned forest.

It is unrealistic to assume that all excavators using burns (or forests) could simultaneously exist at their maximum densities on 1 area. Two species cannot coexist on the same limiting resource (Hardin 1960). We have demonstrated that, although there was overlap, these excavators did not use exactly the same resources; the nest sites of most species differed in nest tree characteristics and in surrounding stand characteristics. Species using the most similar resources nested in burns where snags probably were not so limiting. One area probably could not provide optimum combinations of both nest site and foraging habitat for all species at once. To illustrate, the sum of the maximum breeding densities of each excavator recorded on any plot in any year re-

ported in *American Birds* censuses was 104 pairs/40 ha. The maximum density of excavators on any single census was 42, 2.5 times lower than the total computed using the maxima of each species. It is not realistic to manage any forest type for the maximum possible density of all species occurring in that type. Rather, one could manage for the maximum of selected species (e.g., those restricted to burns such as pygmy nuthatches and Lewis' woodpeckers) and reduced proportions of other species (such as those occurring in both burned and unburned forest), or for some lower proportion of all species. Thomas et al. (1979) recommended planning for a minimum of 40% of the maximum potential population; the results of the *American Birds* census analysis support this management objective. The maximum total density from actual censuses averaged 45% of the theoretical maximum.

*Unburned Forest.*—Most of the above discussion about burned forests also applies to unburned forests. The major difference is that unburned forests produce replacement snags as live trees die. Management should provide a sustained yield of suitable snags in unburned forests.

At Sagehen Creek, 6 excavators and the brown creeper nested in unburned pine-fir forest. Of these, 4 species nested only in unburned types (Fig. 3, Table 30). Potential density of these 7 species combined was 64 pairs/40 ha, 3.6 times higher than the maximum we actually censused. We calculated that 342 suitable snags/40 ha (114 hard, 228 soft) were required to support the potential density of these forest species (Table 31). Providing 228 soft snags would require up to 876 hard snags, given rates of fall typical of the Sagehen Creek basin. Most of these (768) would be necessary for the hairy woodpecker. In 1977, the Unburned and Goshawk study plots had total densities of 340 and 139 suitable snags/40 ha, respectively, yet both plots supported identical combined densities of excavators and creepers (25 pairs/40 ha, Table 29). The Goshawk plot census results suggested that the estimated snag density requirement was too high, but

longer term comparisons of the 2 plots would be necessary to determine if the Unburned plot contained surplus snags and if the Goshawk plot would continue to support bird densities equivalent to those on the Unburned plot. In addition, these densities were of snags only; 37% of the nests of excavators and creepers nesting in unburned forest were in live trees. Thus, live trees with broken or dead tops suitable for nesting should be added to total snag density. This may account for some of the discrepancy between theoretical requirements and actual snag availability.

The superabundance of snags on the Burned study plot in the early years following the Donner burn was associated with cavity-nesting bird densities similar to or lower than those of the past few years (Fig. 25). Bird populations on burned forests at Sagehen increased with increasing snag density up to about 7.5 snags/ha. No such comparison was available for the unburned forest; we cannot document bird density in relation to periods of superabundant snag density. Whether the yearly bird fluctuations on the Unburned plot (Fig. 25) represented variation constrained by snag density, weather, or by territorial behavior was unknown.

The population model (Fig. 26) for a burned forest demonstrated relationships that are equally applicable to unburned forest, except that snag density does not fall to zero eventually in an unburned forest. An important constraint suggested by this model is availability of suitable winter habitat for roosting and foraging. Severe weather conditions reduce resident bird populations to densities that are dependent upon the quantity and quality of winter habitat. Ligon (1971) and Skorupa (pers. commun.) have emphasized the importance of winter habitat for the red-cockaded woodpecker. Haapanen (1965:190) stated that "severe weather and lack of food is the most decisive factor limiting the populations of the (hole nesting) species wintering in coniferous stands." Graber and Graber (1979) have shown that winter mortality was highest among bird

populations that exceeded winter carrying capacity the most. They suggested that "there is a limit to the number of birds of a species that can expect to obtain a survival level of sustenance in a given habitat" (Graber and Graber 1979:100). Thus, winter habitat requirements of resident birds are a crucial concern for future research. It may be that the management of cavity-nesting birds should focus on winter rather than breeding habitat, at least where winters are harsh.

## Snag Recruitment

Conserving snag-dependent wildlife in managed forests requires planning for replacement of snags as they fall. Opportunities for snag recruitment exist with most silvicultural practices, even if natural tree mortality rates are too low to support an abundance of wildlife.

Timber stand improvement includes the removal of cull or damaged trees and tree thinning to maximize wood growth. Timber stand improvement programs often are detrimental to snag-dependent wildlife. Those trees >38 cm dbh, which otherwise would be removed, can be killed and left standing to provide snags. Damaged or unmerchantable trees <38 cm that will not have an adverse effect on growing stock can be left alive until they are >38 cm and then killed. In this way, snags can be created throughout a rotation cycle.

Even-aged management includes clear-cutting, seed tree, and shelterwood harvesting systems. The usual practice following a clearcut is to cut and burn all nonmerchantable residual trees. Instead, the largest diameter residuals can be killed at periodic intervals and left standing. If sufficiently large, these snags will remain standing during most of the next rotation. If the clearcut has no suitable residuals, or if most snags have fallen early in the rotation, snags can be created or existing snags can be conserved along the edge of the cut, preferably in small clumps. Seed tree and shelterwood systems provide these same opportunities for snag recruitment.

Large-diameter snags can be created by killing and leaving some of the seed or shelter trees during the final overstory cut. Snag longevity can be increased by conserving dead-topped or broken-topped live trees, or by killing only the top portion of selected live trees. Such trees do not rot at ground level. The roots are still alive, and these trees will provide nesting habitat much longer than a completely dead tree.

Uneven-aged management includes selection cutting or small patch cuts. Because mature trees are always present, natural mortality can produce new snags and the canopy will protect existing snags against windfall. When natural mortality is too low, snags can be created with minimum financial loss by killing cull, genetically inferior, diseased, or other unmerchantable trees.

The length of the rotation cycle is of critical importance under both even and uneven-aged silvicultural systems because rotation length determines tree diameter. At present, merchantable trees are 40 cm dbh or larger, but as economic incentives for shorter rotations increase, as more mills accept smaller stock, and as other economic incentives stimulate shorter rotations, trees may be harvested when they reach only 30 cm dbh. These small diameter stands will not produce the >38-cm snags required for nesting unless selected trees or patches are allowed to grow beyond the rotation. On good sites, this means an extra 10–20 years; on poor sites trees may have to be retained an extra 50 years or more.

Retention of old-growth stands within managed compartments is an alternative to selected tree retention. Old-growth stands support a high density and variety of cavity-nesting birds (Mannan 1980) and other forest wildlife, primarily because of the high number of large-diameter snags they provide. Retention of old-growth stands will mitigate for unavoidable losses of cavity-nesting bird habitat on intensively managed stands and should be encouraged as a high priority in the management of all forest wildlife.

## RECOMMENDATIONS FOR FURTHER RESEARCH

### Winter Studies

Perhaps the most critical subject for further research is evaluation of cavity-nesting bird populations during winter. Questions for winter studies include:

1. Can additional weather variables improve the correlation between annual precipitation and yearly fluctuations of bird density?
2. To what extent are yearly bird density variations a result of emigration, immigration, or overwinter mortality?
3. What habitat characteristics determine minimum overwinter density and survival?
4. What are the characteristics of roost trees and cavities? Do roost trees differ from nest trees, thereby requiring separate management consideration?
5. How do winter foraging patterns of birds compare to those in other seasons (e.g., Conner 1981, Brawn et al. 1982). How does foraging behavior change with daily weather fluctuations (e.g., Grubb 1975).
6. What are the patterns of home range and territoriality among resident cavity-nesters in winter?

### Foraging Behavior

Our studies indicated that snags are an important foraging substrate used by bark-foraging and flycatching birds, but many more questions are raised than answered. For example:

1. How dependent on snags are birds for foraging? Are snags simply preferred or are they required by some species?
2. What is optimum spacing of snags (or other substrates) for foraging? How does the distance birds fly between foraging sites vary with the quality of those sites?
3. What characteristics define foraging site quality? How do prey densities vary

with bark condition, tree size, tree species, or snag age?

4. Does home range size of any species change with quantity and quality of snags available for foraging?
5. What is the minimum number of snags required for foraging per pair of birds of each species?

### Nesting Behavior

Studies of characteristics of nest sites selected by cavity-nesting birds should be carried out in a range of forest types over a broad area. Such studies, involving comparisons of the same bird species in different types, should reveal the range of acceptable nest conditions and the flexibility of bird preferences over a wide range of snag characteristics. Alternatively, long term experiments at 1 or more sites may be designed to test for flexibility in nesting requirements.

The determination of nest productivity (clutch size and nestling survival) in relation to nest site characteristics, particularly diameter and height, is a special need. Some authors (e.g., Evans and Conner 1979) have suggested that hard snags prevent losses to predators because firm wood resists attempts by larger mammals to expose nestlings. Tree hardness, then, might be another important characteristic affecting nest productivity. Other research questions include:

1. How does cause of tree death affect the potential value of a snag for nesting? Does cause of death influence the species of wood decay fungi?
2. What species of wood decay fungi are associated with the excavation sites of woodpeckers and nuthatches?
3. Can live trees be girdled and inoculated with wood decay fungi to produce nest trees as suggested by Conner (1978)?
4. What is the variability in size of nesting territory defended by each excavator?
5. What environmental factors and morphological features are correlated with territory size of excavators?

### Bird Population Dynamics

Several aspects of cavity-nesting bird population dynamics require much more detailed study and analysis:

1. To what extent do territory sizes relate to maximum breeding density of birds? If breeding bird density is limited by territorial behavior, what are the year-round habitat requirements of non-breeders? Will these birds require special management consideration, or will management for a theoretical maximum breeding population allow sufficient numbers of snags to support non-breeders as well?
2. What are the minimum land area and bird population size required for a self-sustaining population? What are the genetic consequences of managing for a minimum self-sustaining population?
3. What is the shape of the curve relating cavity-nesting bird density to snag density in different forest types? A concave shape (a logistic curve, for example) leads to an underestimate of snag requirements if the real relationship is linear. A more precise description of this curve will be necessary to estimate the response of birds to alternate snag management plans.

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APPENDIX

Scientific names of plants and animals mentioned in text.\*

Common name	Scientific name
BIRDS	
American kestrel	<i>Falco sparverius</i>
American robin	<i>Turdus migratorius</i>
Black-backed woodpecker	<i>Picoides arcticus</i>
Brewer's sparrow	<i>Spizella breweri</i>
Brown creeper	<i>Certhia americana</i>
Chipping sparrow	<i>Spizella passerina</i>
Common nighthawk	<i>Chordeiles minor</i>
Dark-eyed junco	<i>Junco hyemalis</i>
Dusky flycatcher	<i>Empidonax oberholseri</i>
European starling	<i>Sturnus vulgaris</i>
Fox sparrow	<i>Passerella iliaca</i>
Green-tailed towhee	<i>Pipilo chlorurus</i>
Hairy woodpecker	<i>Picoides villosus</i>
House wren	<i>Troglodytes aedon</i>
Lazuli bunting	<i>Passerina amoena</i>
Lewis' woodpecker	<i>Melanerpes lewis</i>
Mountain bluebird	<i>Sialia currucoides</i>
Mountain chickadee	<i>Parus gambeli</i>

APPENDIX

Continued.

Common name	Scientific name
Mountain quail	<i>Oreortyx pictus</i>
Mourning dove	<i>Zenaida macroura</i>
Northern flicker	<i>Colaptes auratus</i>
Pileated woodpecker	<i>Dryocopus pileatus</i>
Pygmy nuthatch	<i>Sitta pygmaea</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>
Red-cockaded woodpecker	<i>Picoides borealis</i>
Tree swallow	<i>Tachycineta bicolor</i>
Western bluebird	<i>Sialia mexicana</i>
White-breasted nuthatch	<i>Sitta carolinensis</i>
White-headed woodpecker	<i>Picoides albolarvatus</i>
Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>
Yellow warbler	<i>Dendroica petechia</i>

INSECTS

Jeffrey pine beetle	<i>Dendroctonus jeffreyi</i>
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TREES

Douglas-fir	<i>Pseudotsuga menziesii</i>
Incense-cedar	<i>Libocedrus decurrens</i>
Jeffrey pine	<i>Pinus jeffreyi</i>
Lodgepole pine	<i>Pinus contorta</i>
Mountain hemlock	<i>Tsuga mertensiana</i>
Quaking aspen	<i>Populus tremuloides</i>
Red fir	<i>Abies magnifica</i>
Sugar pine	<i>Pinus lambertiana</i>
Western larch	<i>Larix occidentalis</i>
Western white pine	<i>Pinus monticola</i>
White fir	<i>Abies concolor</i>

SHRUBS

Sagebrush	<i>Artemisia tridentata</i>
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FUNGI

Red belt fungus	<i>Fomes pinicola</i>
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\* Bird names follow American Ornithologists' Union (1982).